SYSTEMATICS
OF THE MACROURID FISHES

by

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DECLARATION

All the material in this dissertation represents my own independent research. It does not include work that was done in collaboration, or that has been submitted elsewhere in candidacy for any other qualification

S. W. Wood

Abstract

The systematics of rattail fishes (Teleostei: Gadiformes, Macrouridae) is reexamined focussing on the *Coryphaenoides* group of genera, including *Albatrossia*, *Lionurus*, *Chalinura* and *Nematonurus*. The data matrix consists of 69 osteological characters based on personal observations, 17 characters, generally of the soft anatomy, from various published sources and 34 characters reported from peptide mapping of muscle-type lactate dehydrogenase.

An evolutionary systematics of morphology requires, firstly, a historical concept of homology and secondly, a scientific basis for the recognition of patterns. Viewing the organism as a hierarchy of constraint, homology is a relationship of development constraint inherited by parts of organisms. Taxa are types, relationships of constraint inherited by organisms. If, from the morphological perspective, taxa are relationships not groups, conventional concepts of monophyly and related terms cannot apply to them. In practice they describe comparisons between trees. The creation/discovery of patterns is embedded in the practice of systematics and has its basis in the intelligent abilities of human beings. Morphology deals with the linguistic aspect of evolution, rather than with its dynamic genetic aspect. Dynamic and linguistic aspects are complementary yet incompatible. The scientific status of morphology is shown to rest on this principle of complementarity.

Through cladistic analysis of a large number of published characters, I investigate the scenarios and relationships of gadiform fishes that have recently been proposed. The results of the rattail analysis are thus placed within the broader context of gadiform ecology and evolution. In cladistics, parsimony plays the role of Popper's empirical concept of simplicity, as a method of estimating the hypothesis of highest empirical support. Assumptions are made about the likely pathways of evolution in the way the characters are coded. Original classifications of the Gadiformes and the Macrouridae are proposed. Within the gadiforms there is a general trend from jaw precision to jaw protrusion. An index of protrusion/precision shows a negative correlation with depth. Rattails show low values of the index indicating high jaw protrusion. However, within the family the trend is towards higher jaw precision, and the precision/protrusion index is positively correlated with maximum depth.

The discovery of cartilage in the exoskeleton of rattail fishes was an unforeseen result of the method of preparation. In rattails alcian blue reveals hyaline cell cartilage at the margins of certain dermal elements where it is gradually replaced by bone.

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I thank Tomio Iwamoto for a considerable gift of specimens from the California Academy of Scienes. Mark McGrowther at the Australian Museum, Sydney, and Yuri Shcherbachev at the P.P. Shirshov Institute of Oceanology donated specimens of Coryphaenoides serrulatus and C. subserrulatus. Nigel Merrett provided specimens from cruises during the summers of 1992 and 1993. Invaluable advice on practical methods came from Jim Chambers, Oliver Crimmen, Patrick Campbell, Gordon Howes and Ken Joysey. Gordon Howes was responsible for my early coaching on the anatomy of fishes, and Mike Coates gave additional advice and encouragement. Paul Upchurch generously gave me the use of his scanner to help with the figures.

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Abbreviations of Anatomical Terms

A - adductor muscle

An - anal

aa - anguloarticular

ac - anterior crest of fifth infraorbital

ach - anterior ceratohyal

art - articular process (of premaxilla, maxilla)

as - anterior strut of hyomandibula

asc - ascending process (of first infraorbital, premaxilla)

bb - basibranchial

bo - basioccipital

br - branchiostegal ray

C - caudal

cb - ceratobranchial

cl - cleithrum

cor - coronoid ramus of dentary

cp1 - first central protuberance of preoperculum

cp2 - second central protuberance of preoperculum

d - dentary

D - dorsal

dl - distal lamina of first epibranchial

eb - epibranchial

ect - ectopterygoid

ent - entopterygoid

epo - epioccipital

ethc - ethmoid cartilage

exo - exoccipital

f - frontal

fl1 - first horizontal flange of parasphenoid

fl2 - second horizontal flange of parasphenoid

hb - hypobranchial

dhh - dorsal hypohyal

hsp - haemal spine

hyo - hyomandibula

hyoc - hyomandibular condyle of operculum

IAC - interarcual cartilage

ic - intercalar

ih - interhyal

io - infraorbital

iop - interoperculum

lam - lamina

le - lateral ethmoid

lemp - mesethmoid process of lateral ethmoid

lew - lateral ethmoid wing

lf - lateral flange of preoperculum

lr - lateral ridge of frontal

ls - lateral shelf of palatine

m - maxilla

me - mesethmoid

met - metapterygoid

mh - maxillary head

mp - medial process of palatine

not - notch (of hyomandibula, fourth branchiostegal)

op - operculum

opp - opercular process of hyomandibula

p - process

pXI - process for ligament XI (ethmo-maxillary)

pal - palatine

par - parietal

pb - pharyngobranchial

pch - posterior ceratohyal

pcl - postcleithrum

pec - pectoral

pelv - pelvic

peri ossn - perichondral ossification

pext - posterior extension of fifth infraorbital

pm - premaxilla

pmp - postmaxillary process

pop - preoperculum

pr - palatine prong

pro - prootic

ps - parasphenoid

pto - pterotic

pts - pterosphenoid

ptt - posttemporal

q - quadrate

qb - quadrate body

qp - posterior process of quadrate

ra - retroarticular

rc - rostral cartilage

RLA - ramus lateralis accessorius

sh - *sternohyoideus* muscle

sop - suboperculum

spo - sphenotic

sw - swelling

sym - symplectic

tp - thin plate of hyomandibula

tpl - toothplate

uh - urohyal

v - vertebra

vp - ventral process of first hypobranchial, first epibranchial

vhh - ventral hypohyal

vo - vomer

Introduction

The aims of the present study are set out as follows:

First aim (Chapters 1, 2 and 5)

To examine the systematics of the rattail family (Teleostei: Gadiformes, Macrouridae) through the analysis of skeletal characters, specifically to discover new characters and apply rigorous methods of analysis.

Second Aim (Chapter 3)

To understand the links between systematics, morphology and evolution, to justify that it is possible to have an evolutionary systematics of morphology.

Third Aim (Chapter 4)

To establish general themes in the ecology and evolution of gadiform fishes in order to provide the necessary context to understand the ecology and evolution of rattails.

Fourth Aim (Chapter 6)

To investigate thc implications of the results of staining techniques used in the preparation of skeletal material for theories of the vertebrate skeleton.

A reexamination of rattail systematics was the original aim. Rattails are dominant fishes of the world ocean, with over 300 species representing some 30 genera. Intergeneric relationships are poorly known and the placement of one particular group of 60 or so species poses special problems. They are variously grouped under four subgenera of a single genus, *Coryphaenoides* (Iwamoto and Stein, 1974) or are maintained as the distinct genera, *Coryphaenoides*, *Chalinura*, *Lionurus*, *Nematonurus* (Marshall and Iwamoto, 1973). Together *Coryphaenoides*, in the broad sense, is represented by species occupying all bathymetric levels from the upper slope to abyssal soundings. All authors have tended to agree that the genera are more closely related to one another than to any other genus in the family. However, questions have been raised recently by Iwamoto and Sazonov (1988), who suggest that, although *Nematonurus*, *Lionurus* and *Chalinura* form a monophyletic group, *Coryphaenoides* itself may be paraphyletic with respect to *Caelorinchus* and *Macrourus*. The species *Macrurus pectoralis*, often placed in *Nematonurus* (e.g. Okamura, 1970b) is maintained as a separate genus, *Albatrossia*. Iwamoto and Sazonov's cladistic analysis of characters commonly employed in keys and generic descriptions is a step forward towards resolving the problems of rattail systematics.

Okamura (1970b) is the first comprehensive study of the internal anatomy of the macrourid fishes. The study is centred on that portion of macrourid diversity found off the coasts of Japan. The summary of macrourid genera provided by Marshall (1973) for the series *Fishes of the North-Western Atlantic* is more useful for this project because it is based on the same collection, that at the Natural History Museum in London (BMNH). There I have also had access to the specimens prepared by Gordon Howes for his study of the muscles and ligaments of rattails (Howes, 1988). Howes provides a novel insight into the relationships of macrourid genera through an investigation of a number of myological and arthrological characters, but concludes as follows: 'The intrarelationships of the morphologically diverse genera assigned to the Macrourinae [the main subfamily of the Macrouridae] have yet to be worked out cladistically. Myological characters have not been rewarding in this regard, and synapomorphies must be sought in other soft anatomical (particularly in the structure of the light organs) and skeletal features.' The cue for the thesis was taken from these concluding words.

The characters used in the rattail analysis come from a number of sources. There are sixty-nine osteological characters, some of which overlap with those used in Okamura (1970b) but many of which are new. Seventeen characters, generally of the soft anatomy, are taken from Marshall (1973), Iwamoto and Sazonov (1988), Howes (1988) and Iwamoto (1989). Wilson, Siebenaller and Davis (1991) provide 34 characters obtained by peptide mapping of muscle-type lactate dehydrogenase. All available characters are phenotypic. Genotypes have not been sampled for rattails, nor have protein sequences which can under certain assumptions be converted into DNA sequences.

Three subsidiary projects have emerged in the course of the work, each with important bearings on it. However, as the fourth is more anatomical rather than systematic, it constitutes something of an appendix to the dissertation. The second and third projects are concerned with investigating more deeply the meaning of the results from a systematic study, in particular one based largely on skeletal characters. For example, some might see a systematic investigation as involving intimately a discussion of evolution, others might see it as more a question of providing diagnoses and keys of species and genera. I have ignored the latter approach, as it appears unfruitful for determining the relationships among species. The tendency there is to give characters that separate similar species or genera, to avoid confusion during identification. However, the characters that link taxa are often not even stated, or where they are provided by the author they are only recently being rigorously investigated. The improvement made by Iwamoto and Sazonov (1988) is clear.

As far as the first approach is concerned, the relationship between systematics and evolution is not straightforward. The chapter devoted to morphological systematics and evolution comprises three sections, on the concepts of monophyly, parsimony and hierarchy. The section on hierarchy has two strands. The first strand is homology. An evolutionary systematics of morphology requires a historical concept of homology, but criticisms of such a concept have been raised (summarised by Wagner, 1989b). I demonstrate the profit of regarding the organism as a hierarchy of constraint (after Allen and Starr, 1982). Under this view, and equivalent to the proposals of Nelson (1989), homology is seen as a relationship of development constraint shared by parts of organisms. Taxa are seen as types, sets of constraints (homologies) inherited by organisms. Being relationships not groups, conventional concepts of monophyly cannot apply to taxa. This ties up with the conclusion of the section on monophyly, that formal definitions of monophyly and related terms are not equivalent to those given by Hennig (1966) but instead describe comparisons between trees.

The second strand of the hierarchy section, very much related to the first, deals with patterns. An evolutionary systematics of morphology requires a scientific basis for the recognition of patterns. If similarity of form is seen as entirely superficial or even subjective, the ultimate understanding of which comes from developmental genetics, then the science of morphology has no foundation. I discuss how the creation/discovery of patterns is embedded in the practice of systematics and how this process has its basis in the intelligent abilities of human beings. Morphology deals with the linguistic aspect of evolution, rather than with its dynamic genetic aspect. Dynamic and linguistic aspects are complementary yet incompatible (Pattee, 1978). The scientific status of morphology is shown to depend on this principle of complementarity.

The method I employ for the data analysis is the cladistic method, derived from that of Hennig (1966) but much developed since then. The data matrix is assembled in Microsoft Excel 5.0 and analysed by Hennig86 (Farris, 1988). The cladistic method is the usual one for discrete morphological characters. Trees found are of minimum length, that is, of all possible trees they cost the fewest evolutionary steps. This criterion, commonly called parsimony, appears at first sight to be a model of evolution and, as such, appears suspect. Friday (1987) has discussed how such a model is implied by Darwin's principle of divergence. However, parsimony does not act in cladistic analysis like a model, but more like what would be called in statistics a method of estimation. The section on parsimony is therefore a defence of the criterion as identical to Popper's empirical concept of simplicity, a means of determining the empirical support of competing hypotheses. In the hierarchy section I show that assumptions are made about the likely pathways of evolution in the way the characters are coded. This has recently been realised by Maddison (1994).

The muscles and ligaments of rattail fishes are discussed by Howes (1988) as part of a review of functional scenarios and historical relationships of gadiform fishes. Howes arrives at some controversial conclusions, particularly with regard to the scope of the Macrouridae. Three families are removed, namely Euclichthyidae, Bathygadidae and Trachyrincidae, and placed among the gadoids. Howes later recanted his realignment of the Trachyrincidae, but the removal of the two other genera has been supported by Markle (1989) and Sazonov and Iwamoto (1992) respectively. I investigate the scenarios and relationships hypothesised by Howes through the analysis of a number of characters presented in the volume accompanying the Workshop in Gadiform Systematics (Cohen, 1989). In addition, many characters are included from the papers of Howes since WOGADS, where he reexamines his novel conclusions. The broader picture of gadiform systematics results, describing the position of the Macrouridae within the order.

The Macrouridae in the narrow sense is well-defined, with a number of diagnostic characters. Two given by Howes (1988: 6-7) are the presence of a nasal-maxillary ligament, and the connection between the maxillary-premaxillary ligament to the rostral cartilage. Marshall (1973: 502) used the position of the olfactory bulbs, 'well removed from the forebrain' to characterise the Macrouridae. Howes (1989: 123) records that the position of the olfactory bulbs varies greatly in gadiforms from adjoining the forebrain to within the nasal capsule and ascribes this variety to a forward shift of the olfactory bulbs during development. He concludes that 'an ontogenetic anterior shift of olfactory bulbs may be synapomorphic for a broader group of "paracanthopterygians" or independently derived in each group.' Attributing the character to any particular subgroup is therefore unjustified at present. The olfactory bulbs are listed by Howes (1989: 123) as the first of four possible synapomorphies of the Macrourinae, and may be deleted from the list. Character 2, restriction of the opening between the operculum and first gill arch restricted by the buccopharyngeal lining, is taken from Marshall (1965: 304; 1973: 506) and Okamura (1970a: 36; 1970b: 19) and is indeed restricted to the Macrouridae. Character 3, ctenoid scales, is found in Macrouroididae (Okamura, 1970a: 13) and Trachyrincidae (Okamura, 1989: 131; Iwamoto, 1989: 167-168). Character 4, the reduced first dorsal fin spine, is also found in *Macruronus*, the Bathygadidae, Trachyrincidae, Euclichthyidae, Steindachneriidae and Moridae (Marshall and Cohen, 1973: 497; Okamura, 1989: 131; Inada, 1989: 201-202, table 1). Iwamoto and Sazonov (1988: figure 1) and Iwamoto (1989) describes four more diagnostic characters of the Macrouridae: anal fin more developed than second dorsal, distinct gap between dorsal fins, outer gill rakers on 1st arch tubercular to somewhat flat-papilliform or entirely absent, differentiated scutes and ridges on head.

Patterson (1977) established the theory of two skeletons in vertebrates, the dermal exoskeleton and the primarily cartilaginous endoskeleton. According to Patterson, cartilage has not been substantiated in the dermal skeleton of lower vertebrates, but is well documented in birds and mammals. The discovery of cartilage in the exoskeleton of rattail fishes was an unforeseen result of the method of preparation with interesting implications for understanding the development and evolution of the vertebrate skeleton. Alcian blue has been shown to react with hyaline-cell cartilage (Benjamin, 1990), and this form of cartilage has been found to contribute to the exoskeleton in the atheriniform *Poecilia sphenops* (Benjamin, 1989a). In rattails hyaline cell cartilage appears to be involved in the development of certain dermal bones. It exists originally at the margins of certain dermal elements where it is gradually replaced by bone. This process of secondary osteogenesis has also been inferred in the cypriniform *Garra taeniata* (Benjamin, 1989b).

Chapter 1.1: Preparing Cleared and Stained Specimens

Ten batches of cleared and stained specimens were prepared (see Chapter 1.2). The schedule followed for the preparation of the specimens was derived from one produced by Mr Jim Chambers of the Zoology Department, Natural History Museum, which he in turn derived from Dingerkus and Uhler (1977). His colleague, Mr Oliver Crimmen, gave useful advice in the development of my schedule, which is as follows:

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Before starting, make a measurement reflecting the size of the specimen. For macrourids head length should be used, that is, the distance from the tip of the snout to the furthest point of the gill cover.

1. BMNH specimens registered before 1945 were not fixed in formalin, so if preparing a specimen registered before that date fix it formalin. Wash for 24 hours in distilled water.

2. Dissolve 1g of alcian blue solid in a mixture of 700ml 70% industrial methylated spirit (ethanol plus methanol) and 300ml glacial acetic acid. Stain the specimen with alcian blue for up to 24 hours, depending on its size. If desired the specimen may be removed, washed with 70% alcohol and examined under the microscope to assess the extent of staining. If the specimen is stained more darkly in areas of the skeleton rather than muscle then this is an indication that the cartilage has stained fully. Wash off excess stain with absolute alcohol.

3. Take the specimen through a series of alcohols at increasing dilution, leaving it at each stage for 24 hours: 70% alcohol; 1 part 70% alcohol, 1 part distilled water; 1 part 70% alcohol, 2 parts distilled water.

4a. Wash in distilled water.
4b. Retain in distilled water until the specimen sinks.

5a. Put in 1 part sodium tetraborate buffer, 2 parts distilled water. The sodium tetraborate makes the flesh soft and easy to dissect. If the specimen has a lot of flesh, particular around the shoulders, but is otherwise quite fragile, dissection in tetraborate is recommended. In any case eyes and viscera may be usefully removed.

5b. Add a teaspoon of trypsin per 100ml sodium tetraborate buffer. Place in water bath if necessary, but keep the temperature down at about 25°C. The solution will change colour and a blue or green colour indicates that the specimen is successfully digesting.

6. Watch carefully for signs of disintegration, which may happen before the specimen has cleared fully. Change the solution after up to 3 days, depending on the smell, and repeat.

7. Dissolve two pellets of potassium hydroxide in 200ml distilled water. Add enough alizarin red solution to make a deep purple solution. Leave for up to 24 hours.

8. Leave to wash in a solution of potassium hydroxide for 24 hours.

9. Take the specimen through series of glycerins at increasing dilution, leaving it at each stage for 24 hours: 10%, 25%, 50%, 100%. 50% is a suitable working strength of glycerin. Only go on to the 100% stage when the specimen is to enter permanent storage.

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9. Take the specimen through series of glycerins at increasing dilution, leaving it at each stage for 24 hours: 10%, 25%, 50%, 100%. 50% is a suitable working strength of glycerin. Only go on to the 100% stage when the specimen is to enter permanent storage.

Chapter 1.2: Material Prepared and Examined

Species	Register number	HL/mm
Batch 1. 11/91		
11 *Coryphaenoides rupestris*	1993.9.13:1	ca. 27
Batch 2. 10/12/91 to 17/1/92		
21 *Coryphaenoides rupestris*	1981.3.16:379	27
22 *Coryphaenoides guentheri*	2 ex 1991.7.9:237-320	27, 28
23 *Lionurus filicauda*	1887.13:98-103	28
24 *Lionurus carapinus*	1990.8.3:229-230	25
25 *Chalinura leptolepis*	1990.8.21:192-210	30
26 *Hymenocephalus italicus*	1973.3.5:18-23	26
Batch 3. 8/1/92 to 15/4/92		
31 *Echinomacrurus mollis*	1993.9.13:10-19	40
Batch 4. Lots 1-5, small specimens, 17/1/92 to 15/4/92		
Lots 6-8, large specimens, 17/1/92 to 21/5/92		
41 *Cynomacrurus piriei*	1963.2.1:6	31*
42 *Odontomacrurus murrayi*	1963.2.1:9	24*
43 *Nematonurus armatus*	1991.7.9:105-107	35
44 *Sphagemacrurus hirundo*	1986.4.22:6-7	28
45 *Cetonurus globiceps*	1986.4.22:4-5	36
46 *Malacocephalus laevis*	1928.9.18:42-45	50
47 *Caelorinchus c. caelorhincus*	1973.10.29:209-222	54
48 *Mataeocephalus microstomus*	1939.5.24:723-724	52
Batch 5. 20/5/92 to 13/8/92		
51 *Coryphaenoides rupestris*	1993.9.13:2	ca. 61

* Skeleton did not survive trypsin digestion

Batch 6. 3/8/92 to 7/9/92		
61 *Chalinura leptolepis*	1993.9.10: 47-48	36, 38
62 *Lionurus filicauda*	1887.13:98-103	27
63 *Nematonurus armatus*	1993.9.10:42	37
Batch 7. 1/3/93 to 7/4/93		
71 *Nematonurus armatus*	1993.9.8:6-7	44, 47
72 *Hymenocephalus italicus*	1973.3.5:18-23	34
73 *Malacocephalus laevis*	1973.3.5:26	31
74 *Macrourus berglax*	1965.6.22:8-9	63
Batch 8. 26/5/93 to 6/8/93		
81 *Chalinura brevibarbis*	1993.9.10:49	39
82 *Nematonurus yaquinae*	1993.9.10:43	53
Batch 9. 24/8/93 to 8/12/94		
91 *Coryphaenoides zaniophorus*	1993.9.10.27-28	42, 54
92 *C. serrulatus serrulatus*	1993.9.10:21-22	44*, 50*
93 *C. serrulatus oceanus*	1993.9.13:7	38
94 *C. subserrulatus*	1993.9.10:25-26	48*, 49*
95 *C. capito*	1993.9.10:9	55*
96 *C. ariommus*	1993.9.10:5-6	57, 62
97 *C. anguliceps*	1993.9.10:3	67
98 *C. mexicanus*	1971.10.22:24-26	56
Batch 10. 2/94 to 27/6/94		
101 *Echinomacrurus mollis*	1993.9.13:10-19	ca. 70
I made a single skeletal preparation:		
Coryphaenoides rupestris	1993.9.13:3	ca. 60

*Skeleton did not survive trypsin digestion. Radiographs showed that specimens no longer possessed an ossified skeleton.

The list below gives the remaining BMNH material examined. The folowing abbreviations are used to describe material:

CS - cleared and stained

D - dissected

X - radiographed

Percopsidae: *Percopsis omiscomaycus*, 1973.3.20:46-48 (CS); *P. guttatus*, 1892.12.30:371-373 (CS).

Aphredoderidae: *Aphredoderus sayanus*, 1898.12.29: 141-148 (6 specimens, X), 1898.12.29: 149 (CS), 1898.12.29: 150 (SK).

Amblyopsidae: *Amblyopsis spelaea*, 1846.12.14:1, 1847.10.18:6, 1849.11.6:1, 1851.11.20:1, 1858.5.10:1 (CS, X).

Carapidae: *Carapus acus*, 1952.11.25:1-4 (CS); *C. bermudensis*, 1985.6.6:138-183 (CS).

Ophidiidae: *Ophidion rochei*, 1971.12.17:6-8 (CS).

Bythitoidei: *Oligopus ater*, 1977.12.19:2-4 (CS).

Batrachoididae: *Opsanus beta*, 1948.8.6:1399-1400 (CS).

Lophiidae: *Lophius piscatorius*, 1970.2.17:633 (CS).

Melanonidae: *Melanonus zugmayeri*, 1991.7.9:731 (CS).

Trachyrincidae: *Trachyrincus trachyrincus*, 2 ex 1976.7.30:42-55 (CS), 1 ex 1976.7.30:42-55 (CS).

Macrouroididae: *Macrouroides inflaticeps*, 1939.5.24:684 (D, CS gill arches).

Macrouridae: *Nezumia aequalis*, 1973.3.5:60-64 (CS); *Trachonurus villosus*, 1963.2.25:226-228 (CS); *Malacocephalus laevis*, 1904.11.30:33 (SK); *Ventrifossa sp.*, 1965.2.25:61-71 (CS); *Coryphaenoides* rupestris, 1887.12.9:82 (SK); *Caelorinchus caelorhincus*, 1905.2.2:18 (SK); *Caelorinchus caribbaeus*, 1963.2.25:244-250 (CS);

Euclichthyidae: 3 ex 1986.5.14:1-3 (X).

Moridae: *Lepidion eques*, 1981.3.16:437-444 (CS).

Bregmacerotidae: *Bregmaceros sp.*, 18 ex unreg. (CS), 1957.12.2:5-12 (CS).

Gaidropsaridae: *Gaidropsarus mediterraneus*, 2 ex unreg. (CS), 2 ex unreg. (CS); *G. vulgaris*, 3 ex unreg. (SK).

Phycidae: *Phycis blennoides*, 1898.4.30:14 (SK); *Urophycis regia*, 1985.6.6:109-119 (CS).

Ranicipitidae: *Raniceps trifurcus*, 1884.8.26:3 (SK).

Chapter 1.3: Outline Cranial Dissection of a Macrourid

As a guide to dissection, the skull was divided into seven systems of bones: neurocranium, infraorbitals, jaws, hyopalatine, operculars, hyoid arch, branchial arches. In the schedule that I devised, given below, the 7 systems are dissected in order, with the exception of system 1. The dermal roofing bones are removed at the beginning, whereas the neurocranium proper is exposed at the end.

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For each bone, expose, clearing away muscle and connective tissue, draw *in situ*, noting connections to neighbouring bones (ligamentous or direct), and then remove.

1. Dermal roofing bones

Dissect the bones separately or as a pair depending on how well they are fused together. The other bones of system 1 are dissected at the end.

2. Infraorbitals

Dissect the ascending process of the first infraorbital from the ligamentous contact between the lateral ethmoid and the palatine.

Dissect away the skin covering the sensory canal along to the angle of the preoperculum and up to the otic capsule.

Take care not to damage remnants of the bony roof of the infraorbital canal, particularly the lateral plate of the first infraorbital.

3a. Upper jaw

Note the ligaments from the maxilla, attaching to the mesethmoid and nasal, and from the premaxilla to the palatine. Cut the ligaments to free the lower jaw and the hyopalatine system.

If the premaxillae grip the rostral cartilage, then dissect them out as a pair.

3b. Lower jaw

Take care to dissect the articular head of the quadrate from the anguloarticular, as well as the strong ligamentous connection between the heel of the retroarticular and the interoperculum.

4. Hyopalatine

Note the articulation between the hyomandibula and the otic capsule.

Turn the hyomandibula on end to view the hyomandibularis nerve pathway.

Cut the interhyal away from the interspace of cartilage between the symplectic and hyomandibula.

5. Operculars

Dissect the preoperculum from the hyomandibula and the posterior process of quadrate.

Dissect the operculum from the condyle of hyomandibula, and remove it along with the interoperculum and fragile subopercular from the surrounding connective tissue.

6. Hyoid arch

The ventral hypohyals are ligamentously connected to one another and to to the urohyal, and lie in contact with the hypobranchials.

The head of the urohyal is attached to the basihyal, which effectively forms the most anterior element of the basibranchial series.

Clear away the *sternohyoideus* muscle which, as a rule, runs from the urohyal to the pectoral girdle.

7. Branchial arches

Dissect an arch at a time, starting with the dorsal elements. Take particular care with the delicate first epibranchial.

1. Neurocranium

Cut Baudelot's ligament and remove the pectoral girdles. Separate the posttemporal from the supracleithrum of the girdle on each side.

Dissect the first neural arch from the occipital region. (The exoccipitals contact the zygapophyses and the basioccipital the centrum.)

***

A data matrix of 69 characters was assembled from observations on 23 macrourid species. The assembly took several steps. Firstly, following the dissection method recorded above, I made drawings and descriptions of the 7 systems for the four type species of the *Coryphaenoides* group, namely *C. rupestris*, *Lionurus filicauda*, *Chalinura leptolepis* and *Nematonurus armatus*. Outgroup species were added, *Hymenocephalus italicus*, *Malacocephalus laevis* and *Caelorinchus caelorhincus*, and the first data matrix was assembled and the first cladistic analysis was performed. As specimens of

new species were examined, the character concepts I had proposed provisionally were submitted to testing, adjusted if necessary and the characters reanalysed. Through this cycle of illumination, described in Chapter 3.3.3, I increased the number of examined species and honed the character list to that given in Chapter 2.1. The drawings placed after the text represent my own camera lucida drawings of the many rattail specimens examined. These serve to justify my character concepts. In Chapter 2.2 I list 17 characters, mainly from the soft anatomy, which I have drawn from published sources. The data matrix of all 86 morphological characters is given in Table 1.

Chapter 2.1: Osteological Characters

System 1: Neurocranium

(1) Nasals fused into a single bone, or closely adjoined:

0 = no (Figure 1A); 1 = yes (Figure 1B)

(2) Downward extension of nasal:

0 = shallow (Figure 2A); 1 = deep (Figure 2B)

(3) Ossification of lateral ridge of frontal:

0 = good (Figure 3A); 1 = reduced or absent (Figure 3B)

(4) Processes on mesethmoid for ethmo-maxillary ligament (unordered):

0 = sharp processes (Figure 4A); 1 = rounded swellings (Figure 4B); 2 = stubby (Figure 4C); 3 = cylindrical (Figure 4D)

(5) Swelling around ethmoid cartilage forming articulation with lateral ethmoid:

0 = absent (Figure 4A, 4C, 4D); 1 = present (Figure 4B)

(6) Width of mesethmoid process w.r.t. height of lateral ethmoid wing:

0 = wide (Figure 5A); 1 = narrow (Figure 5B)

(7) Number of pairs of horizontal lateral flanges strengthening bottom of braincase:

0 = two (Figure 6A); 1 = one (Figure 6B)

(8) Shape of pterosphenoid:

0 = semicircular (Figure 7A); 1 = extended ventrally (Figure 7B)

(9) Degree of overlap between exoccipitals:

0 = long (Figure 8A); 1 = short or absent (Figure 8B)

(10) Shape of basioccipital:

0 = diamond-shaped (Figure 8); 1 = balloon-shaped (Figure 9)

System 2: Infraorbitals

(11) Shape of first infraorbital, comparing length by depth (Figure 10):

0 = long; 1 = moderate; 2 = short

(12) Ascending process of first infraorbital:

0 = tall, strong (Figure 10A); 1 = low, weak (Figure 10B)

(13) Posteroventral extension and crest of fifth infraorbital:

0 = present (Figure 11A, 12); 1 = absent (Figure 11B, 11C)

(14) Development of anterior crest of fifth infraorbital:

0 = poorly-developed (Figure 11B, 11C, 12A); 1 = well-developed (Figure 11A); 2 = deep channel (Figure 12B); 3 = anterior and posterior crests meet to form tube (Figure 12C)

(15) Fifth infraorbital flat, anvil-shaped:

0 = no (Figure 11A, 11B, 12); 1 = yes (Figure 11C)

(16) Sixth infraorbital narrow, deep channel:

0 = no (Figure 11A, 11B, 12A); 1 = yes (Figure 12C)

System 3: Jaws

(17) Teeth extend beyond postmaxillary process of premaxilla:

0 = yes (Figure 13A); 1 = no (Figure 13B)

(18) Height of premaxillary ascending process as percentage of ramus length (Figure 13):

0 = <=62%; 1 = 70%; 2 = 82-85%; 3 = 93%; 4 = 116-118%;5 = 225%

(19) Height of postmaxillary process:

0 = high (Figure 13, 14A); 1 = low (Figure 14B, 14C)

(20) Length of postmaxillary process of premaxilla:

0 = short (Figure 14A, 14C); 1 = long (Figure 13, 14B)

(21) Arch between maxillary head and articular process:

0 = absent (Figure 15A, 15C); 1 = present (Figure 15B)

(22) Notch in posterolateral portion of maxilla:

0 = small (Figure 15B, 15C); 1 = deep (Figure 15A)

Anterior border of coronoid ramus:

0 = has concavity (Figure 16A); 1 = straight (*Lionurus filicauda*, Figure 16B)

(23) Slope of retroarticular:

? = posteroventral (Figure 17A); 0 = vertical to slightly anteroventral (Figure 17B); 1 = well anteroventral (Figure 17C)

(24) Perichondral ossification of retroarticular:

0 = thin lamina produced posteriorly from perichondral ossification to form posterior border (Figure 17, 18A, 18C, 18D); 1 = lamina largely absent, perichondral ossification itself forms most of posterior border (Figure 18B)

Horizontal part of retroarticular anteriorly:

0 = not downturned (Figure 17, 18A, 18B, 18D); 1 = downturned (*Lionurus filicauda*, Figure 18C)

(25) Boss of bone on retroarticular acting as site of attachment for mandibular-interopercular ligament:

0 = absent (Figure 17A, 17C, 18A); 1 = present (Figure 17B, 18B, 18C, 18D)

(26) Boss of bone, if present

0 = above base (Figure 17B, 18D); 1 = at base (Figure 18B, 18C)

System 4: Hyopalatine

(27) Medial process of palatine:

0 = absent (Figure 19A); 1 = present (Figure 19B, 19C, 19D)

(28) Palatine boss high and narrow, set at large angle to prong:

0 = no (Figure 20A); 1 = yes (Figure 20B)

(29) Lateral shelf extends posteriorly beyond posterior perichondral ossification, posterior portion embayed:

0 = no (Figure 20); 1 = yes (Figure 21)

(30) Development of lateral shelf:

0 = weak (Figure 20B); 1 = strong (Figure 20A)

(31) Shape of entopterygoid:

0 = dorsally enlarged (Figure 22A, 22B, 22C); 1 = rectangular (Figure 22D)

(32) If enlarged, pentagonal:

0 = no (Figure 22A); 1 = yes (Figure 22B, 22C)

(33) Entopterygoid posteriorly embayed within metapterygoid:

0 = no (Figure 23A); 1 = yes (Figure 23B)

(34) Process of ectopterygoid which contacts posterior perichondral ossification of palatine:

0 = absent (Figure 24A); 1 = present (Figure 24B, 24C)

(35) Medial expansion of the process, if present:

0 = negligible (Figure 24B); 1 = significant (Figure 24C)

(36) Length of metapterygoid greater than depth:

0 = no (Figure 25A); 1 = yes (Figure 25B)

(37) Posterior process of quadrate:

0 = sharp; 1 = distally rounded

(38) Area of contact between posterior process of quadrate and preoperculum very broad:

0 = no (Figure 23A, 23B); 1 = yes (Figure 23C)

(39) Anterior strut of hyomandibula:

0 = small (Figures 26A, 26B); 1 = large (Figure 26C, 26D)

(40) Notch in ventral surface of hyomanidibula:

0 = absent (Figure 26A, 26C); 1 = present (Figure 26B, 26D, 27)

(41) Thin plate, lamina produced anteriorly from medial surface of hyomandibula:

0 = present (Figure 27A); 1 = absent (Figure 27B)

System 5: Operculars

(42) Number of central protuberances of preoperculum:

0 = one (Figure 28A); 1 = two (Figure 28B)

(43) Lateral flange of preoperculum (unordered):

0 = generalised (Figure 29A); 1 = projects backwards (Figure 29B); 2 = poorly ossified, large (Figure 29C); 3 = broad and roof-like (Figure 28C)

(44) Hyomandibular condyle of operculum:

0 = bears process (Figure 30A); 1 = lacks process (Figure 30B)

(45) Shape of interoperculum:

0 = broad (Figure 31, 32); 1 = elongate (Figure 33)

(46) Dorsal concavity of interoperculum:

0 = absent (Figure 32A); 1 = present (Figure 31, 32B, 33)

(47) Shape of interoperculum, posteriorly:

0 = tapering (Figure 31, 32, 33C); 1 = club-shaped (Figure 33D)

(48) Ventral concavity of interoperculum:

0 = absent (Figure 31, 32, 33A, 33B); 1 = present (Figure 33C, 33D)

System 6: Hyoid Arch

(49) anterior ceratohyal, comparing smallest width by length:

0 = narrow (Figures 34A, 34B); 1 = broad (Figure 34C)

(50) Interdigitation between anterior and posterior ceratohyals:

0 = present (Figure 34); 1 = absent (Figure 35)

(51) Anterodorsal part of lateral surface of anterior ceratohyal tucked in to meet dorsal hypohyal:

0 = no (Figure 35); 1 = yes (Figure 34)

(52) Interior perichondral ossification of dorsal hypohyal:

0 = present (Figure 36A); 1 = absent (Figure 36B)

(53) Posterior lamina of interhyal extended ventrally:

0 = yes (Figure 37A); 1 = no (Figure 37B)

(54) Number of branchiostegal rays:

0 = 7; 1 = 6

(55) Head of fourth branchiostegal ray:

? = not expanded; 0 = expanded, without notch (Figure 38A); 1 = expanded, with notch on posterior surface (Figure 38B)

(56) Shape of urohyal (unordered):

0 = *Melanonus* type (Figure 39A); 1 = *Hymenocephalus* type (Figure 39B); 2 = *Caelorinchus* type (Figure 40A); 3 = *Macrourus* type (Figure 40B)

System Branchial Arches

(57) Shape of first hypobranchial, comparing greatest length by greatest width:

0 = long (Figure 41B); 1 = short (Figure 41A)

(58) Ventral process of first hypobranchial:

0 = absent (Figure 41A); 1 = present (Figure 41B)

(59) Proximal perichondral ossification of second hypobranchial:

0 = lamina produced from part (Figure 42A); 1 = produced from whole (Figure 42B, 42C)

(60) Proximal perichondral ossification of second hypobranchial, if lamina produced from whole:

0 = well from part (Figure 42B); 1 = produced well from whole (Figure 42C)

(61) Process on first ceratobranchial:

0 = absent (Figure 43A); 1 = present (Figure 43B)

Process on second ceratobranchial:

0 = absent; 1 = present (*Macrourus berglax*)

(62) Process on third ceratobranchial:

0 = absent (Figure 43A); 1 = present (Figure 43B)

(63) Process on fourth ceratobranchial:

? = absent; 0 = present, slight (Figure 44A); 1 = present, distinct (Figure 44B)

(64) Ventral process of first epibranchial:

0 = absent (Figure 45A, 45B); 1 = present (Figure 45C, 45D, 45E)

(65) Distal lamina of first epibranchial

0 = small (Figure 45C, 45D, 45E); 1 = large (Figure 45B)

(66) Ventral process of first epibranchial, if present:

0 = small (Figure 45E); 1 = large (Figure 45C, 45D)

(67) Ventral process of first epibranchial, if present:

0 = rounded (Figure 45C); 1 = narrow (Figure 45D)

(68) Toothplate of third epibranchial:

0 = fused to bone (Figure 46B, C); 1 = not fused (Figure 46A)

(69) Toothplate of third epibranchial, if fused:

0 = long (Figure 46B); 1 = short (Figure 46C)

Chapter 2.2: Published Characters

I have searched a number of published sources for characters bearing on the relationships of the genera of rattails, especially *Coryphaenoides*. A list of the characters I have abstracted from the literature is given below. I make use of the following abbreviations to refer to particular contributions:

is - Iwamoto and Sazonov (1988: figure 1)
h - Howes (1988: table 1; 1989: figure 10)
iwa - Iwamoto (1989: 170)

(70) Marshall (1973: 533) - anal and urogenital openings encircled by broad band of naked black skin, situated far from anal fin origin
0 - no; 1 - yes

(71) Marshall (1973: 499) - jaws and mouth (p. 499)
0 - large, terminal or subterminal
1 - small, inferior

(72) Marshall (1973: 504) - vagal lobes of brain well-developed, mouth and pharynx richly covered in taste buds
0 - no; 1 - yes

(73) Marshall (1973: 509) - drumming muscles of swimbladder
0 - in neither sex; 1 - in males only

(74) is4 - spinous 1D ray
? - absent; 0 - smooth; 1 - serrated

(75) is13 - number of retia mirabilia
0 - 2; 1 - 4; 2 - 5-7

(76) is15 - outer gill rakers on first arch
0 - present; 1 - absent

(77) is16i - light organ

0 - absent; 1 - rudiment present; 2 - present

(78) is16ii - external form of light organ

? – light organ absent or no external sign of light organ; 0 – tubular; 1 – bulbous

(79) is17 - head

0 - normal; 1- inflated

(80) is19i - scale patches on gular membrane

0 - present; 1 - absent

(81) is19ii - dorsal surface of head

0 - fully scaled; 1 - naked areas either side of snout

(82) is19iii - underside of snout

0 - fully scaled; 1 - naked or sparsely scaled

(83) is22 - jaws

0 - moderate to large, mouth opening unrestricted; 1 - short, mouth opening restricted posterolaterally by lip folds

(84) h4/14i - rectus communis attachment

0 - inserts (entirely) on uh; 1 - fully attached to sh

(85) h5 - A1

0 - incompletely divided into A1a and A1b; 1 - divided into A1a and A1b; 2 - divided into A1a, A1b and A1c

(86) iwa21 - dentition in both jaws

0 - homodont; 1 - heterodont

Chapter 3.1: Monophyly and Comparisons between Trees

Farris (1974) devised a method for assessing the empirical status of groups, proposing formal definitions of monophyletic, paraphyletic and polyphyletic groups. I would like to examine the revised treatment of the Farris method for deducing the status of groups given recently by Farris (1991: 298-299). I present this treatment below:

Consider a tree *T* which shows the relationships of certain members of a group *G* to each other and to certain non-members of *G*. Suppose that the members of group *G* show state 1 of character *k* and the other terminals of tree *T* show state 0. If the root node of *T* can be unambiguously assigned state 0 of *k* and *k* requires no homoplasy on *T*, then *k* is unique and unreversed on *T*. In this case, group *G* is a monophyletic group. It is an empirically justified component of *T*. Now let us specify *G* with an abstract variable called its indicator. All members of *G* take value 1 of the indicator and non-members value 0. Given a particular tree the indicator of *G* can be treated like character *k* in order to determine the status of *G* on that tree. Group *G* is monophyletic if value 1 of its indicator behaves as a synapomorphy, polyphyletic if multiple origins of that value are required, and otherwise paraphyletic.

I would like to make a simple point concerning the meaning of the expression 'behaves like a synapomorphy'. Consider a systematist studying a grouping *G* which is conventionally accepted as being defined by state 1 of character *g*. For the following data matrix, taxa W and V constitute G (see Figure 47A):

	g	h	i
Z	0	0	1
Y	0	0	1
X	0	1	0
W	1	1	0
V	1	1	0

In the course of testing the group G, the systematist discovers that state 1 of *g* is found not only in those species traditionally included in *G*, but also in species U. In the mind of the researcher the group *G* is thus extended to *G'*. However, if the full data for species U are as follows, group *G'* is not corroborated in the analysis (see Figure 47B):

	g	h	i	j
Z	0	0	1	1
Y	0	0	1	0
X	0	1	0	0
W	1	1	0	0
V	1	1	0	0
U	1	0	1	1

State 1 of *g* requires homoplasy. But *G* is nonetheless justified by the greater weight of evidence. State 1 of *g* defines *G* and is a synapomorphy in that sense, but also requires multiple entries on the tree. Is *G* monophyletic or polyphyletic? If we accept Farris' (1991) account, then we have a paradox: the defining character of *G*, its 'synapomorphy', does not 'behave as a synapomorphy'. It is not both unique and unreversed. Nevertheless, it is obvious that the set of species traditionally included in *G* has been corroborated as a monophyletic group. Once the analysis has been completed, this can be ascertained without any recourse to real characters, but only to the topology of the resulting tree.

Comparing trees

The indicators of Farris (1991), the group membership characters of Farris (1974), are equivalent to the cluster descriptor variables of Farris (1973). In the latter paper, Farris aimed to produce a measure of the similarity in the shapes of a pair of trees, i.e. a tree comparison metric (see Penny and Hendy, 1985; Swofford, 1991).

Descriptor variables are assigned to the clusters of a reference tree, the members of each cluster being given a value 1 and non-members value 0. The cluster descriptor variables are then mapped on to the comparison tree. If a cluster's descriptor variable shows homoplasy, i.e. extra steps, on the comparison tree then the cluster is nonmonophyletic. Farris (1973) allows the cluster descriptor variables to 'evolve' on the comparison tree according to Camin-Sokal parsimony (Camin and Sokal, 1965) because it is easier to implement than Wagner parsimony (Farris, 1970). Camin-Sokal parsimony is constrained such that reversals are forbidden. In this case, if a reference cluster's descriptor variable requires homoplasy in order to be mapped on to the comparison tree, the extra steps required take the form of multiple entries. Wagner parsimony is unconstrained and if extra steps are

required to accommodate a reference cluster on the comparison tree then these may take the form of either parallelisms or reversals. The use of Wagner parsimony illustrates the link between cluster descriptor variables and group membership indicators. If the extra steps take the form solely of reversals then the cluster is paraphyletic. If the extra steps take the form at least partly of parallelisms then the cluster is polyphyletic.

Cluster distortion method

Farris (1973) divides the number of extra steps required by a descriptor variable on the comparison tree by the maximum possible number of extra steps. The result of this division Farris calls the *single cluster distortion coefficient*. It can be shown that the value of this coefficient is equal to (1-ri) where ri is the retention index of the cluster descriptor variable on the compared tree. The retention index is defined by Farris (1989) as follows:

$$ri = \frac{g-s}{g-m}$$

m = minimum number of steps the character can show on any tree

s = actual number of steps the character shows on the tree in question

g = maximum number of steps the character can show on any tree

$$1 - ri = 1 - \frac{(g-s)}{g-m} = \frac{g-m-g+s}{g-m} = \frac{s-m}{g-m}$$

The quantity $(s-m)$ equals the number of extra steps required by a cluster descriptor variable to be accommodated on the comparison tree, and the quantity $(g-m)$ is equal to the maximum number of extra steps required. The single cluster distortion coefficient, scdc, is thus equal to $(s-m)/(g-m)$ that is (1-ri).

In the case of cluster descriptor variables, which are simple binary variables, g is equal to the number of terminals belonging to the cluster in the reference tree. The minimum number of steps, m, is equal to one less than the number of states and in this case is therefore equal to 1. The formula for the single cluster distortion coefficient can thus be simplified as follows:

$$scdc = \frac{s - 1}{n - 1}$$

s = actual number of steps shown by cluster descriptor variable on comparison tree

n = number of terminals included in reference cluster (or at least, number of such terminals that appear in comparison tree)

To provide an overall measure for the similarity between a pair of trees, Farris suggests averaging the individual cluster distortion coefficients. However, an ensemble cluster distortion coefficient can easily be provided by (1-RI), where RI is the ensemble retention index.

RI is calculated in the same way as the individual retention indices, but the sums of *m*, *s* and *g* over all characters are used.

ensemble distortion coefficient $= \frac{S - M}{G - M}$ S = sum of extra steps needed by each descriptor variable

$= \frac{S - K}{N - K}$ N = sum of number of terminals included in each cluster

K = number of clusters

An example of the use of the cluster distortion method is given in Figure 48. The trees 48B and 48C are compared with tree 48A. The descriptor variables for each of the 10 clusters of tree 48A are coded as a data matrix. Tree 48C requires 9 extra steps and Tree 48B requires 15. The RI for 48B and 48C are 0.50 and 0.70, giving ECDC of 0.50 and 0.30 respectively. The statistics for each of Tree 48A's descriptor variables are shown below:

actual steps for each descriptor

	1	2	3	4	5	6	7	8	9	10
48B	2	1	3	3	3	3	3	3	2	2
48C	1	1	1	1	1	2	3	4	3	2

maximum steps for each descriptor

	1	2	3	4	5	6	7	8	9	
48B and 48C	3	2	7	8	7	6	5	4	3	2

retention indices for each descriptor

	1	2	3	4	5	6	7	8	9	10
48B	0.50	1.00	0.33	0.50	0.60	0.60	0.50	0.33	0.50	0
48C	1.00	1.00	1.00	1.00	1.00	0.80	0.50	0	0	0

single cluster distortion coefficient

	1	2	3	4	5	6	7	8	9	10
48B	0.50	0	0.67	0.50	0.40	0.40	0.50	0.67	0.50	1.00
48C	0	0	0	0	0	0.20	0.50	1.00	1.00	1.00

Now let us define G as comprising not only species W and V as in Figure 47, but also species Q, P and N. G therefore corresponds to the seventh cluster of Tree 48A. On both Tree 48B and 48C the cluster descriptor of G requires two extra steps. However, in the case of 48B one of the extra steps takes the form of a parallelism. G is therefore polyphyletic on Tree 48B. The cluster descriptor of G requires two reversals on Tree 48C. G is therefore paraphyletic on 48C.

Agreement and discrepancy between trees

Farris' (1973) method of assessing the similarities between trees has a close link with the method used by Novacek et al. (1988). According to the latter authors, agreement between a reference tree and a comparison tree for a particular group occurs when that group is monophyletic in both. Two cases of discrepancy are identified, (i) where the reference group is polyphyletic in the comparison tree and (ii) where the group is paraphyletic. Novacek et al. (1988: 59) provide both verbal and algebraic descriptions of these cases. Simplified descriptions are given below:

Agreement - reference group is monophyletic

All members of the group chosen from the reference tree are assigned to the same component of the comparison tree and themselves constitute that component.

The reference group's descriptor variable does not require extra steps on the comparison tree. The reference group's membership indicator is unique and unreversed.

Case (i) discrepancy - reference group is polyphyletic

The members of the reference group are assigned to different components of the comparison tree.
The reference group's descriptor variable requires extra steps on the comparison tree, some of which take the form of multiple entries. The group membership indicator is not unique and may be reversed.

Case (ii) discrepancy - reference group is paraphyletic

The members of the reference group are assigned to the same component of the comparison tree, but themselves do not constitute that component.
The reference group's descriptor variable requires extra steps, which are exclusively comprised of reversals. The group membership indicator is unique but reversed.

Farris defined paraphyly

Farris (1991) has returned to Hennig's original rationale for distinguishing between paraphyly and polyphyly: 'The aim of completely severing paraphyly and polyphyly from characters is inherently ill-conceived ... Without characters, paraphyly and polyphyly mean nothing' (Farris, 1991: 304; see Hennig, 1966: 146). Farris has abjured one of the advantages of the method as he published it in 1974. The Farris 1974 method can be seen to reflect Nelson's (1971) insight that monophyly and its related terms are used in comparisons between branching diagrams, in other words that 'the definitions should refer only to "cladistic aspects" such as normally depicted in diagrams of relationships - not to definitions (suites of characters)' (Nelson, 1973: 310). This point should have become clear in the preceding sections, with regard to the formal equivalence of group membership indicators and cluster descriptor variables. Definitions of monophyly and related terms based on the behaviour of real characters were rejected so as to avoid the problem of groups being potentially both paraphyletic and polyphyletic depending on their particular character justification (Nelson, 1971: 471; 1973: 310; Platnick, 1977a: 195-196). Group membership indicators are instead fictional in the technical sense defined by Harré (1972: 80). They relate to real characters and their evolution 'roughly as novels to histories.' Group membership characters are treated like real characters, according to the logic of a particular parsimony algorithm, but they are 'artificial', 'abstract' products of the imagination (Farris, 1973: 52; 1991: 28).

The definitions of paraphyletic and polyphyletic groups proposed by Nelson (1971) and Oosterbroek (1987) are what might be called exclusion definitions. Nelson defines a paraphyletic group as a monophyletic group from which a single monophyletic group or species has been excluded. Even if the excluded group consists of a number of monophyletic subgroups, since these are not disjunct the excluded group is still regarded as single not multiple. A polyphyletic group results from the exclusion of multiple subgroups or species. These must not be nested within each other but instead be disjunct. Nelson's definition suffers because intuitively paraphyletic groups, such as the Reptilia, are regarded as polyphyletic (Farris, 1974: 549). In other words, the Reptilia is treated as polyphyletic even though it is hypothesised to have a single not a multiple evolutionary origin. Similar, and even worse problems occur with Oosterbroek's definitions (see Farris, 1991: 300-301).

Before giving his formal definitions of paraphyly and polyphyly, Farris (1974) provides a set of 'preliminary definitions'. A paraphyletic group is defined as an incomplete monophyletic group in which the most recent common ancestor is included. A polyphyletic group is similarly an incomplete monophyletic group, but one from which the most recent common ancestor has been excluded. The definitions of Ashlock (1971, 1973) also involve this distinction. Nelson (1973) treats such a distinction as illogical, because each ancestral species 'is purely hypothetical, unrepresented by specimens in collections, unnamed, and nomenclatorially nonexistent; consequently it is not a member of any taxon of any system of classification - phylogenetic or otherwise' (Nelson, 1973: 310). Ax (1987) comments that the assignment of an ancestral stem species to a nonmonophyletic group, even if actually possible, is inappropriate because nonmonophyletic groups 'include only part of the descendants of their latest common stem species and correspondingly, cannot include this stem species' (Ax, 1987: 180). The formal definitions of Farris (1974) avoid this contentious issue, necessarily involved in the attempt to provide a phylogenetic distinction between different types of nonmonophyletic groups. The definitions are based solely on the behaviour of abstract variables, which describe comparisons between branching diagrams. In fact, the Farris 1974 method provides a totally general means of comparison. Branching diagrams of any sort can be compared, including phenograms for instance (Farris, 1973; 1991: 299).

Chapter 3.2: A Defence of Popperian Parsimony in Cladistics

The nature of parsimony in cladistics has again come under scutiny. Methods that offer different means of chosing the optimal cladogram for a data set are now available. There is always a danger that the new methods may be taking cladistics away from its aim, to produce theories of relationship with the highest possible explanatory power. Kluge (1993) makes this charge against three-taxon statement analysis (Nelson and Platnick, 1991); Kluge and Wolf (1993) challenge taxonomic congruence or consensus. Ultimately, the alternative methods question the identity of parsimony, and optimality, in cladistics as truly and appropriately of Popper (1959). Here I seek to provide support for the case presented by Kluge (1993) and Kluge and Wolf (1993) through a clarification of the relationship between Popperian parsimony and cladistics. I start by identifying two ideals of classification, a novel expression of the conclusions reached in the seminal paper by Farris (1980). I go on to show that they jointly express Popper's ideals of simplicity and explanatory power. Finally, I attempt to justify this conclusion to authors who have argued for a different meaning of parsimony in cladistics, namely Beatty and Fink (1980), Johnson (1982) and Crisci (1983).

Generality and parsimony

Nelson (1979) divided cladistic analysis into three stages: fundamental, derivative and general. The fundamental stage of character analysis (Nelson discussed only component analysis) involves the collection of representative specimens of the species to be studied. In the derivative stage characters are conceptualised and the character states for particular species recorded. The general stage involves the use of a parsimony algorithm to generate a cladogram and to discover the defining characters of groups. In moving from one stage of classification to the next the focus of the analysis shifts. Three focal contexts can therefore be described, corresponding to a particular stage of the analysis.

Each stage of character analysis involves a different kind of character pattern. A fundamental pattern is the holomorphology of a species (Wiley 1981). It consists of the observed features of all morphological variants of the species, which are at this stage not yet conceptualised. A derivative pattern is a similarity (or derivative character state) shared by a number of species. A general pattern consists of homologies (general character states) defining a hierarchy of groups.

The extent of a character state's derivative pattern can be describes as its level of generality, in other words the generality of propositions that can be made on the basis of that character state. A character state's optimum level of generality, the level at which the generality of propositions made on the basis of that state is maximised, corresponds to the level in a hierarchical classification which embodies the information on this character state. In other words, the information on the character state is concentrated at this hierarchical level (Farris 1980: 500).

The Tetrapoda even though defined by 'legs' includes snakes, among other groups, which lack legs. In order to allow for exceptions it is better to think in terms of predictions rather than propositions. Thus, 'legs' is placed at the hierarchical level corresponding to the Tetrapoda in order to maximise the generality of *predictions* made on the basis of that character state. Farris (1980: 512) states that for the most natural and informative classifications, the total number of exceptions to predictions 'will be as small as is possible for the data.'

The level of generality is therefore considered optimum when the following two conditions are met:
(i) The generality of predictions made on the basis of the character state is maximised.
(ii) Exceptions to the predictions made on the basis of the character state are minimised.

In a 'perfect' classification all character states are placed at their optimum level of generality. In other words the derivative patterns are in full correlation or agreement. The two conditions can therefore be called the two ideals of optimal predictive classification. In a real data set the derivative patterns do not form a simple nested arrangement, but overlap. This sort of disagreement between derivative patterns is called incongruence. The extent of some of the overlapping derivative patterns will have to be adjusted to remove the overlap. To accommodate incongruence in a classification, there must be some departure from the two ideals of classification. The correct level of generality for disagreeing character states therefore has to be non-optimum. A set of general patterns results from the maximisation of congruence between derivative patterns.

The level of generality of an incongruent character state is adjusted by the parsimony algorithm in one of two ways (de Pinna 1991: 374). One possible action is to split the derivative pattern of a character state into two derivative patterns of lower generality. The level of generality of the original character state has therefore been adjusted to below its optimum level. The other possible action of the test is to adjust the level of generality of incongruent character states to above their initial level. This, however, requires exceptions to the predictions based on the character states to be noted at a lower hierarchical level.

Simplicity and explanatory power

The two ideals of classification are equivalent to the two components of both Popper's (1959: 141, 145) concept of simplicity and Bunge's (1961: 132) concept of explanatory power. Paraphrasing Bunge (1961, 1967), to ask for maximum explanatory power is to ask for 'maximum range compatible with reasonable accuracy' (Bunge 1967, II: 48). Maximum generality of predictions made on the basis of a character state can be equated with maximum range of that state. Minimum exceptions to predictions can be equated with minimum inaccuracy.

Popper's (1959) concept of simplicity similarly has two components: degree of strictness, 'the degree, as it were, in which a theory imposes the rigour of law upon nature' (Popper 1959: 141), and degree of nonadhocness. 'Thus we are led back, by our concept of simplicity, to ... that rule or principle which restrains us in our indulgence in *ad hoc* hypotheses and auxilliary hypotheses: to the principle of parsimony in the use of hypotheses.' Strictness is easily equated with range and nonadhocness with accuracy. The two ideals of classification therefore state, in Popperian terms, that the strictness of character state hypotheses should be kept at a maximum, while maintaining a minimum of *ad hoc* hypotheses. A parsimony algorithm finds the cladogram with the greatest explanatory power (veracity, Wiley 1981: 239) and with the fewest *ad hoc* hypotheses (Engelmann and Wiley 1977; Farris 1983).

Criticisms of Popperian parsimony in cladistics

Beatty and Fink (1980)

Beatty and Fink (1980) provide an excellent review of Sober (1975) from the point of view of systematists. Their review contrasts Sober's view of simplicity as informativeness with Popper's concept of simplicity as falsifiability. In Sober's calculus, a hypothesis is more simple than another with respect to a particular question, if that hypothesis is able to answer the question in hand with the addition of less information. More information is contained in the hypothesis. It is more informative and more simple in Sober's view. Popper's concept of simplicity derives from his equation of simplicity with empirical support, namely falsifiability. 'But according to Sober, hypothesis support and hypothesis simplicity are distinctly different goals of scientific enterprise. If support was our only goal, then the most satisfactory hypotheses would be those that either reasserted the evidence or described direct consequences of the evidence. Clearly, we seek hypotheses which go beyond the

evidence. We seek more informative - hence simpler - hypotheses. On the other hand, if informativeness was our only goal, then the most satisfactory hypotheses would be wildly bold' (Beatty and Fink, 1980: 646).

We seek hypotheses which are of sufficient range to be informative, but of sufficient accuracy to remain well-supported. In other words, we desire hypotheses of 'maximum range compatible with reasonable accuracy' (Bunge, 1967: II, 48). We desire hypotheses of maximum explanatory power (Bunge, 1961: 132). As explained above, Popper's (1959) concept of simplicity does in fact have the two components of Bunge's formulation of explanatory power. Strictness is range, nonadhocness is accuracy. Beatty and Fink (1980) equate simplicity only with range, and thus with informativeness. However, if the degree of nonadhocness of a hypothesis is also taken into account, Popper's concept of simplicity can be seen to include Sober's notion of empirical support. Simplicity and support are one in Popper's concept.

Crisci (1983)

Crisci (1983: 35) defines parsimony as follows: 'By parsimony I mean a rule instructing the scientist to choose the simplest of several empirically equivalent hypotheses.' Thus Crisci advises that the most parsimonious hypothesis of relationships be chosen, as the simplest 'among empirically equivalent trees, because to do otherwise would commit us to a path which leads toward untestable and ungrounded hypotheses' (Crisci, 1983: 40). This is partly true, since the acceptance of an unparsimonious scheme of relationships will involve a proliferation of *ad hoc* hypotheses. However, Crisci's description of parsimony is at odds with the practice of cladistics. Parsimony is the criterion by which the empirical support of competing theories of relationship is assessed. It is not a last resort when the verdict given by the available evidence is uncertain.

Johnson (1982)

In a similar way to Crisci, Johnson (1982) states that parsimony saves the researcher from 'multiple acceptable explanations ... which remain viable after a period of empirical testing' (Johnson, 1982: 83). She concludes that the use of parsimony as a non-evidential criterion 'to decide which hypothesis should be accepted (however provisionally) as *the most accurate representation of the experienced world* sets a dangerous precedent in the evaluation of scientific evidence' (Johnson, 1982: 83). Use of

parsimony as a non-evidential criterion would indeed set a dangerous precedent. Johnson (1982: 81) quotes Salmon: 'Why should we believe that a simpler hypothesis is more likely to be true than a complex one, given that each has sufficient explanatory power with respect to the facts in question?' (Salmon, 1961: 275). Salmon assumes that given the facts available both simple and complex hypotheses have the same explanatory power. The simpler hypothesis, however as defined by Popper (1959), has the greater descriptive and explanatory power than the complex one in the sense defined by Bunge (1961: 132).

The view held by Johnson (1982) can be seen to derive from the assertion made by Rudner (1961) that '... insofar as the considerations which influence hypothesis acceptance ... can *properly* be called considerations of simplicity they are subjective, while, on the other hand, insofar as they are objective they are only misleadingly called considerations of simplicity' (Rudner, 1961: 117). Rudner proposes a dichotomy between ontological and descriptional (linguistic or methodological) parsimony, which is adopted by both Johnson (1982) and Crisci (1983). Popper's (1959) empirical criterion, where the simplest hypothesis is the most falsifiable, falls outside Rudner's classification and is thus dismissed by Johnson as 'contrary to the current consensus' and involving an '*ad hoc* synonymy of parsimony and falsifiability' (Johnson, 1982: 82). Instead, Rudner (1961) and Johnson (1982) champion Goodman's notion of simplicity: 'Simplicity is systematisation (Goodman 1959) - it is a means of evaluating redundancy and irrelevancy in different hypotheses, and thus it constitutes an advance in the standardisation of scientific method' (Johnson, 1982: 82). What Rudner and Johnson fail to acknowledge is that Goodman (1961) gives an excellent account of simplicity not in terms of systematisation, but in terms of the range and adhocness of hypotheses. Goodman (1961) considers three competing hypotheses:

(1) All maples, except perhaps those in Eagleville, are deciduous
(2) All maples are deciduous
(3) All maples whatsoever, and all sassafras trees in Eagleville, are deciduous.

Although hypothesis (2) is safer than (1) it is preferable to (1) on the grounds of simplicity: 'Insertion of the ad hoc exceptive clause both weakens and complicates the hypothesis' (Goodman, 1961: 150). Hypothesis (3) is bolder than (2) but is not as simple: 'The expansion made in (3) is as unwelcome as the exception made in (1)' (Goodman, 1961: 151). In other words, the expansion brings the hypothesis beyond its acceptable range. The concept of simplicity described by Goodman (1961) is an empirical criterion, a means for deciding the empirical content of competing hypotheses: 'Hypothesis (2), although it lies between (1) and (3) in safety and strength, is more simple and preferable to either'

(Goodman, 1961: 151). Goodman's (1961) concept is identical to the notion of simplicity described by Popper (1959). A better defence of Popper's concept could not be provided.

Summary

The parsimony criterion in cladistics is shown to act according to two ideals of classification. The two ideals can be summarised as follows. The generality of predictions made on the basis of a character state should be the maximum compatible with the minimum number of exceptions to those predictions. It is possible for the two ideals of classification to indicate several possible generalisations of a particular set of derivative patterns.

Beatty and Fink (1980) present Sober's (1975) calculus of simplicity as informativeness. Their analysis shows that Sober's concept expresses only the range of scientific hypotheses, not their accuracy. Popper's concept of simplicity is shown, in fact, to have both these elements. The twin criteria of range and accuracy ensure that simpler hypotheses have greater explanatory power. Crisci (1983) and Johnson (1982) describe parsimony as able to provide a choice between empirically equivalent solutions. However, this conflicts with the use of parsimony as a measure of the empirical support of a hypothesis. Johnson (1982) prefers Goodman's (1959) calculus of simplicity as systematisation but she neglects his later treatment. Goodman (1961) provides an elegant explanation of Popperian parsimony in terms of the range and adhocness of hypotheses.

Chapter 3.3: Hierarchy Theory as the Formal Basis of Evolutionary Theory

3.3.1: Introduction

Science attempts to provide a truly universal language through which to describe the world. The problem is that, as an unfortunate result of ever increasing specialisation, science can become fragmented into different factions with different approaches and different standards for evaluating methods. The fragmentation of scientific language that can result from specialisation is detrimental to the course of science. Each of the factions is impoverished, in that the true depth of implications held by particular facts are not explored. Creative hypotheses are not developed because that would lead the investigator outside his chosen faction. I suggest that the unity of science does not rest in key facts specifically, but in the adoption of a single formal language that is common across different fields. There is no such formal language for biology. Among other things, this hinders the teaching of biology. Too many people are put off by the number of seemingly unconnected facts they have to learn and the general lack of first principles. Fragmentation in science manifests itself as a fragmentation in the language science uses. That language blocks creativity by denying expression of certain research questions, and indeed denying questions of broader philosophical significance. Science, as a search for knowledge rather than just the provider of technology, then becomes divorced from society in general, seeming of little relevance to the rest of reality.

Thompson (1989) views scientific theories simply as interpreted formal systems. A theory has a purely formal basis and becomes a scientific theory proper when a particular interpretation is placed upon it. Thompson (1989) gives a very useful example to illustrate this view of theories. The theory of physical space was challenged indirectly through a challenge on its formal basis. There was no direct challenge, at the empirical level, on the predictions of the theory itself, though these predictions were extended. One of Euclid's postulates, the parallel postulate, was found not to be derivable from the other axioms. Two new systems of curved geometry resulted: hyperbolic geometry and spherical, or Riemannian, geometry. Einstein's theory of general relativity has Riemannian, rather than Euclidean, geometry as its formal basis, adopting a picture of space as curved.

To discover the formal basis of an existing scientific theory, to provide a formalisation or systematisation, is to elucidate the connections between different parts of the theory. The

philosophy of science tells us that *formal simplicity* is one criterion of a good, sound theory (see Goodman, 1959). This contrasts with the empirical simplicity criterion of Popper (1959). From a formal standpoint, a sound theory is well connected; the theory has firm, clear relationships among its parts. If we believe that theories should be tested through hypothetico-deductive logic, as Popper (1959) requires, then how can we test the predictions if we are not sure quite what implications an observation has for the theory as a whole? The practical benefit to be gained from providing a formalisation of a scientific theory is to clarify the relationships between parts of the theory. Particular observations will have unforeseen relevance to areas of the theory outside their normal province. For example, if we say that the properties of a constrained developmental system enable punctuational changes, then we might predict that the cases in which gradual evolution has been observed involve changes which, developmentally, are not significantly constrained. An understanding of the formal basis of a theory will also clarify the particular aims of different approaches to the theory and enable a choice between models.

It is the aim of this paper to propose that the appropriate formalisation of evolutionary theory is provided by the theory of hierarchically organised systems. A hierarchy is defined as a system of communication, where entities are defined by the extent to which they constrain or filter information they receive (Allen and Starr, 1982: 11, 37). Organisms are hierarchies of constraint; elements of the phenotype differ in the extent to which they constrain genetic information. Information flows two ways through a hierarchy, out into the environment and back again (Allen and Starr, 1982: 8-9). On the outward journey of the gene, the constraints of the developmental system produce the characteristic form of the organism. On the homeward journey of the gene, the phenotype acts as a hierarchy of selective constraints, favouring or reducing the chance of the different items of genetic information being passed on to the next generation.

To prove that hierarchy theory is indeed the formal basis of evolutionary theory, it is important to show that the concept of constraint is applicable to the living organism. However, there is an even more striking prediction of a hierarchical formalisation of evolutionary theory: there should exist a biological principle of complementarity equivalent to that found in quantum physics (Pattee, 1978). The second part shows the relationship between concepts of homology and developmental constraint from the viewpoint of systematics. The third part provides a description of cladistic analysis that lays the groundwork for the justification of complementarity in the final part. The fourth part takes the theme of morphological stability as a route into an evolutionary discussion of developmental constraint and its counterpart, adaptational constraint. The final part shows that there are two complementary aspects of

evolutionary history, and a different approach should be used to reconstruct each one. The two approaches differ as to the source of data, method of generating data, model of evolution assumed and form of results produced.

3.3.2: Nelson's concept of homology - a link between cladistic analysis, evolution and development

Nelson (1989) has suggested that instead of taxa being seen as groups of units, such as species or organisms, they should be seen as relationships. A taxon is a relationship inherited by organisms, and a homology, then, is a relationship inherited by parts of organisms. 'Conceived as relationships, taxa and homologies do not literally descend from one another. Taxa come into being with organisms that literally descend' (Nelson, 1989: 281). Through descent with modification, Nelson concludes, organisms and parts of organisms accumulate inherited phylogenetic relationships (cf. Nelson, 1989: 281-282). Descent with modification results in a phylogenetic hierarchy of organisms with inherited relationships.

Nelson's (1989) concept of homology, combined with a hierarchical perspective, is a powerful tool for evolutionary theory. It disposes of the criticisms that have been advanced against the historical concept of homology. For example, Wagner (1989b) lists four criticisms of the historical concept (the first and fourth are in fact the same):

(1,4) Lack of continuity

'Only replicators like genes pass on their own structure to their descendants directly. Morphological structures are not replicators ... The notion of continuity of descent is not problematic for genes but is less clear for organs' (Wagner, 1989b: 55-56).

'Conceived as relationships, taxa and homologies do not literally descend from one another' (Nelson, 1989: 281). Morphological homologies are inherited by parts of the organism's phenotype, and it is the organisms themselves that literally descend. Continuity of descent is possible only for elements of the genotype, but not for elements of the phenotype.

(2) Lack of individuality

'In the simplest case phylogenetic homology is a one-to-one mapping from the characters of one species onto characters of another species. A one-to-one mapping implies that in each species all characters can be recognised individually' (Wagner, 1989b: 57).

The organism, from a hierarchical perspective, is neither an undecomposable whole, nor a fully decomposable 'composite of atoms'. Organisms are *near-decomposable* (see Simon, 1962, 1973; Koestler, 1967: 64-65; Allen and Starr, 1982: 70-74). How does one make sense of elements that, in comparisons across a variety of organisms, cannot be recognised individually? The simple answer is not to focus on one level in the hierarchy as a naive perspective would dictate, but to proceed with the examination at the next level, that of the whole series of elements.

(3) Variability of development

'Phylogenetically homologous characters need not share common pathways of ontogenetic development' (Wagner, 1989b: 58). Between species, the origin of cellular material, the precise sequence of events or specific inducers, have all been found to vary.

If homology is seen as a relationship inherited by parts of organisms, then the variable development of those parts is no longer problematic.

Having discussed problems with the historical concept of homology, Wagner (1989b) proposes an alternative, a biological concept of homology: 'Structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation. These structures are thus developmentally individualised parts of the phenotype' (Wagner, 1989b: 62). Below I shall elaborate how the elements of Wagner's biological definition are embraced by Nelson's (1989) concept of homology.

We have said that homologies are relationships inherited by parts of organisms. However, in hierarchy theory the contrast between wholes complete in themselves and fragmentary, dependent parts is regarded as an illusion. Whether an entity appears as a part or a whole simply depends on the point of view of the observer: from a more inclusive level, the entity appears as a part, from a less inclusive level, as a whole. Constituent 'elements' of an organism are thus simultaneously autonomous wholes and dependent parts, they are *holons* in the sense of Koestler (1967): 'Every holon has the dual tendency to preserve and assert its individuality as a quasi-autonomous whole; and to function as an integrated part of an (existing or evolving) larger whole. This polarity between the self-assertive and integrative tendencies is inherent in the concept of hierarchic order; and a universal characteristic of life. The self-assertive tendencies are the dynamic expression of

holon wholeness, the integrative tendencies of its partness' (Koestler, 1967: 343). The distinctiveness of an element, the fact that we can recognise its identity across numerous organisms, derives from its wholeness, the tendency of a holon to assert itself. If an element cannot be recognised individually, this lack of distinctiveness emphasises the partness of the holon, its tendency to integrate itself among other elements as part of a larger whole, such as a series. The following passage by Bateson may be interpreted in this light: 'The phenomenon of serial resemblance is in fact an expression of the capacity of repeated parts to vary similarly and simultaneously. In proportion as in their variations such parts retain this capacity the relationship is preserved, and in proportion as it is lost, and the parts begin to vary independently, exhibiting differentiation, the relationship is set aside' (Bateson, 1894: 569). When elements of a series vary similarly and simultaneously they cannot be recognised as distinct. They remain parts integrated into the larger whole, the series. When elements differentiate, they become individually recognisable and thus assert themselves as wholes distinct in themselves. To reiterate: whether an element appears as a part or a whole depends on context. Armed with this insight it is possible to extend Nelson's (1989) concept of historical homology to include serial, or more generally, iterative homology. Nelson could equally well be referring to a series of elements. Hence, the iterative homology of a set of parts is imparted to them through the inheritance of the embracing singular homology. The 'scaleness' of the scales of a fish, in virtue of which the individual scales are iteratively homologous, is inherited in the same way as the singular homology 'possessing scales'. It does not matter that the scales of a fish are not individually recognisable. The logical necessity of this position was realised many years ago by Hubbs: 'If we admit the homology between any scale *x* of an individual trout and any scale, say *y* of a salmon, and between this scale *y* in the salmon and scale *z* in the trout, then how can we logically deny that homology exists between scales *x* and *z* on the body of the same trout!' (Hubbs, 1944: 294).

Patterson (1982) describes a contrast between transformational and taxic homology. According to Patterson, taxic homology is the relation that specifies hypotheses of grouping. Nelson's (1989) concept of homologies as relationships is also taxic. Transformational homology is rooted in the concept of ideal or material transformation from a common precursor, and thus subsumes both idealistic and evolutionary concepts of homology. We compare structures with the supposed precursor in the common archetype or common ancestor to judge whether they are homologous. Patterson regards serial homology as a form of transformational homology (Patterson, 1982: 48). He is forced therefore to deny that taxic homologies are repetitive: '... homologies are anatomical singulars (Riedl, 1978, p.52), structures of which there is only one, or a bilateral pair, per organism' (Patterson, 1987: 9). But there is a fudge here, which is nonetheless admirably declared

by Patterson: how can a repetition of structures across the main axis of the animal be logically distinguished from any other form of repetition? Ghiselin (1976) legitimately calls the homology between members of a bilateral pair 'antimeric homology' (Ghiselin, 1976: 139). If this concept is construed transformationally, then we must envisage that structures on the two sides of the animal trace back to single structures in an ancestral one-sided animal! No, iterative homology and historical homology are, as Van Valen (1982) perceived, aspects of the same phenomenon. But that phenomenon is taxic not transformational homology. The concept of transformational homology applies only to the genotype, where material continuity of descent is possible.

If organisms are near-decomposable, they do not consist wholly of individually recognisable parts. We have parts in a context, for example, one element among several of a series. This element, for example the axis vertebra of tetrapods, may later assert itself, weakening its integration into the rest of the series, and become individualised. We can extend the notion of 'parts in a context' in more general terms to the issue of characters versus character states. The character is not simply an abstraction but provides the biological context for its character states. We might take the palatine bone as a character and thus differences in the shape and orientation of the palatine boss and prong reflect evolutionary changes within this context. Character concepts of this 'either/or' sort therefore comprise an aspect of similarity (homogeneity) and aspects of difference (heterogeneity). Teleost fishes are all to some extent homogeneous, since they all have a recognisable palatine (within the context of the palatopterygoquadrate arch), but are also heterogeneous in the extent to which parts of the palatine are developed. 'Presence/absence' characters are simpler. They represent the expression or suppression of the self-assertive tendency of the holon, the acquisition or loss of its individuality. To sum up, character states are designed to document changes in the individualisation of parts of organisms, changes in the balance between similarity and difference, between the integrative and self-assertive tendencies of those parts.

The insight of Nelson (1989) into taxic homology also provides a useful characterisation of Wagner's concept of individualisation: through descent with modification, parts of organisms accumulate inherited taxic homologies, and thus become increasingly individualised. If we remember that 'parts of organisms' can refer to 'series of parts' we can see how the individualisation and differentiation of a particular part of a series involves the inheritance of at least one taxic homology unique to it alone. Wagner repeatedly cites an excellent example of individualisation of members of a series, namely the thorax of insects (Wagner, 1986: 151; 1989a: 1162; 1989b: 63). He says that the thorax most probably arose as a differentiation of segments 7,8 and 9 in the annelid-like ancestors of insects. However, the thorax as an entity in itself is not

homologous to the corresponding segments in annelids or centipedes for example. 'The thorax is the unit differentiated from the rest of the body in terms of appendages and internal anatomy, a condition not found in centipedes' (Wagner, 1986: 151; 1989a: 1162; 1989b: 63). The thorax represents, in the terms of Rieppel (1994), a unique condition of form, or in other words, a new autonomous whole irreducible to its parts.

The thorax has become individualised from the other bodily segments; at the same time the thorax serves to "individuate" the taxon Insecta (in the sense of von Baer, 1828; see Rieppel, 1994: 90). But we must be clear with our language here. Is it the acquisition of the new assertive holon that individuates the new taxon? Not exactly, since a taxic homology is a relation among holons: organismic holons are homologues related by particular homologies (Nelson, 1994: 120). Why is it that we recognise the thorax, in fact? The thorax, as a self-assertive whole, creates its own environment of constraint for its parts (Allen and Starr, 1982: 51), so that these parts do not vary in such a way as to undermine the individuality of the whole. It is possible for such a trend to be reversed, for the balance to swing from heterogeneity back to homogeneity. For example, the prootic and epiotic of reptiles lost their separate individualities and fused to form the mammalian petrosal, which then in its turn has followed its own path of differentiation.

If we say that the thorax is a part which is homologous throughout the insects, then we imply a continuity of descent between the thorax of the ancestral insect and that of the descendant insects. But as Wagner (1989b) points out, continuity of descent is possible only for aspects of the genotype not the phenotype. What we see conserved throughout the insects is the developmental constraint that preserves the individuality of the thorax. The thorax as taxic homology is a developmental constraint inherited by an insect's parts. Indeed, *any similarity that we see across organisms can be considered as a shared developmental constraint.* It is the business of phylogenetic systematics, namely cladistic analysis, to decide the cause of this sharing (Rieppel, 1992, 1994). The cause of the shared developmental constraint is deduced from the overall relationship of the particular constraint to other constraints. The relationship between one character state and other states for a particular study group may be either congruence, in which case the constraint is homologous, or incongruence, in which case the constraint is homoplastic. This judgment of ultimate, historical cause is made without concern for the proximate causes of the constraint in terms of particular developmental mechanisms.

3.3.3: Cladistic analysis - a three-stage discovery procedure

Nelson (1989) refers to cladistics as a discovery procedure. Nelson's intention in bringing the term to systematics appears partly to emphasise the empirical claims of cladistics: 'For Nelson (1989), empirical notions require a "discovery procedure" such as cladistics' (Rieppel, 1991: 93). Relationships that cannot be discovered by cladistics, for example, that between an ancestral species and its descendant species, are deemed non-empirical by Nelson (1989). Let us investigate the richer significance of Nelson's term and delve down to its roots in semiotics, the theory of signs (see, for example, Dunsby and Whittall, 1988: Part IV, where the theory is applied to music). If we wish to discover the meaning of a message, such as a passage of music or a phrase of spoken language, then we need two things: (1) a code, by which we are able to interpret the message, i.e. discover its meaning; and (2) a discovery procedure, by which we discover the code. If we apply this to systematics, then the message is equivalent to a study group of organisms. The code is the means by which we bring meaning to the study group, in terms of meaningful features (similarities) and meaningful similarities (homologies). The code therefore represents the specific characters and the specific hierarchy that comprises them. The discovery procedure is the means of discovering the code, the specific characters and hierarchy. The methodological rules of Rieppel (1988a, b) thus form the discovery procedure of cladistics. The code consists of rules for the interpretation of the structures of the study group, rules in a different sense, namely that of Pattee (1978). Pattee's rules will have great significance when we come to discuss the principle of complementarity, but for the time being we will discuss rules in Rieppel's sense.

Nelson (1979) divides cladistic analysis into three stages. The fundamental stage of character analysis (Nelson discussed only component analysis) involves the collection of representative specimens of the species to be studied. In the derivative stage characters are conceptualised and the character states for particular species recorded. The general stage involves the use of a parsimony algorithm to generate a cladogram and to discover the defining characters of groups. In moving from one stage to the next the focus of the analysis shifts. Three focal contexts can therefore be described, corresponding to a particular stage of the analysis.

Each stage of character analysis involves a different kind of character pattern. A fundamental pattern is the holomorphology of a species (see next section). It consists of the observed features of all morphological variants of the species, which are at this stage not yet conceptualised. A derivative pattern is a pattern of constraint, or similarity, shared by a number of species. A general

pattern describes the pattern of homologies inherited by organisms. Sharing is meaning in the derivative context, and congruence, the nested hierarchical relationship between derivative patterns, is meaning in the general context.

Holomorphologies

Consider the following passage from Beckner (1959). Here he discusses the view of the 'New Systematics' that the biological species is real, whereas higher taxa are not: '... the whole species is, so to speak, bound together in a network, the strands of the net representing potential crosses. These strands are largely confined within the limits of one species. The essential point is that the relation between mates is a biological, dynamic, causal, or if one prefers, real and objective relation ... The relations between the members of higher taxa are not biological, not dynamic, not causal, and in this sense not real and objective; they are historical relations (in so far as the taxa are based upon phylogeny) and relations of abstract morphological similarity' (Beckner, 1959: 67-68). Beckner's discussion agrees with that of Wiley, where he says that taxa are not individuals but historical groups of species (Wiley, 1980: 78; 1981: 75). This view recognises that higher taxa have a class-like quality, but holds to the most obvious evolutionary understanding of taxa as historical entities.

Taking Beckner's view, it is not necessary to limit ourselves to a species concept rooted in interbreeding. According to Eldredge and Salthe (1984: 189) species owe their existence to the production of new entities of like kind from old. This ability of cohesion or 'more-making' (Eldredge, 1985: 144) shows species construed in this way to be individuals. Eldredge and Salthe's definition is in line with the concept of species advocated by Nelson and Platnick (1981: 11), as populations of self-perpetuating organisms: 'In many groups of organisms, for example, we can distinguish samples representing males and females; or eggs, larvae, pupae, and adults. We find, however, that males do not produce other males, or larvae other larvae, so that these samples, by themselves, have no independent existence in nature. Thus the concept of species must include a criterion of self-perpetuation: males and females together; eggs, larvae, pupae, and adults together; form self-perpetuating species.' This 'extended biological' species concept is an very intuitive one. Without the concept it is impossible to speak of an aberrant specimen, a unrepresentative sample, or even of comparable semaphoronts (Hennig, 1966; see Nixon and Wheeler, 1990: 219).

Kluge (1988: 57) has drawn attention to the view of Danser (1950: 118) who was a typologist, that life cycles as a whole should be classified: 'His reason for doing so was simple - it is only natural to think of organisms in their entirety'. This empirical process of ontogeny is the basis of Hennig's (1966) concept of holomorphology: 'The holomorphology of an organism is the total spectrum of characters exhibited by that organism during its lifetime' (Wiley, 1981: 12). The reason for studying the holomorphology of an organism is obvious. A consideration of whole life cycles will reveal that characters absent in late ontogeny are nonetheless present in early ontogeny. For example, the relationship of tunicates with vertebrates was revealed by the discovery of a notochord in the tunicate larval stage. Wiley has generalised Hennig's concept to apply to species, as well as to organisms: 'The holomorphology of a species is the total spectrum of the holomorphology of the individuals comprising that species' (Wiley, 1981: 12). The introduction of the concept of species holomorphology is a natural one, taking into account the processes of ontogeny and tokogeny through which biological populations maintain themselves in nature. However, the concept of species holomorphology derives principally from the observation that a particular organism may not display the representative characters of the self-perpetuating population to which it belongs. Wiley (1981: 119) gives various examples. Alternation of generations in both animals and plants produces complex holomorphologies. A single organism of the sporophyte or gametophyte generation of a moss cannot qualify as a fundamental unit of systematics, since alone it does not form a self-perpetuating population. Mosses must be classified by means of characters from both generations. The caste system found in social insect yields both reproducing and non-reproducing organisms. Each shows a different suite of characters.

The tension between creation and discovery

ladistics, if it is a discovery procedure in the sense of semiotics, is a way of discovering and communicating meanings. If we examine an excellent discussion of the nature of communication provided by McCabe (1987), then a tension is exposed between aspects of creation and aspects of discovery in cladistics. The same tension exists within cladistics that is present in all forms of linguistic communication.

'All life at any level is a matter of communication. Every organism is an organism by virtue of its power of communication. What makes a human body human is that it is involved in linguistic communication' (McCabe, 1987: 118). An animal's environment is organised in terms of the

relevance of the parts of that environment to the animal's activities and needs. The fruits of the animal's exploration turn the animal's environment into its world. An animal's world is organised through its body and its senses, they make the world meaningful to it. 'To share in the interpretation of a world and the response to it is to communicate ... the animal's body is the means of creating or discovering meaning in the environment and thereby turning the environment into a world' (McCabe, 1987: 119). An animal is therefore able to 'realise' meanings in its world, in the sense of 'to discover' and 'to make real' (McCabe, 1987: 120). Meanings are therefore found to be 'real' (discovered) and at the same time made to be 'real' (created). An object has meaning and significance if it has a role in the business of living (McCabe, 1987: 119).

Classifying organisms must be done for pragmatic reasons: to divide up the world into manageable parts to facilitate communication. As human beings we partake in linguistic communication by sharing meanings by means of media which we have created ourselves (McCabe, 1987: 120), and these include formal scientific classifications. Classifications are created as tools in linguistic communication, but nevertheless involve discoveries about the world.

The creation-discovery cycle

Resolution of the tension between creation and discovery is made particularly clear by Checkland and Scholes (1990). They realise that our interactions with the world are cyclical. The cyclic nature of cladistic analysis was described by Hennig (1966) in his famous phrase 'reciprocal illumination', referring to the checking and re-checking of hypotheses. The cyclic illumination of the world that takes place during cladistic analysis has been highlighted recently by Kluge (1991). Human observers create the linguistic tools for understanding organisms. Furnished with these tools, they are able to give nature a proper interrogation and discover her secrets. Cladistic analysis involves a cycle of interrogation and response, of creation and discovery. Cladistic analysis is not simply a discovery procedure, but indeed represents what might be called a 'creation/discovery procedure'.

The legend to Checkland and Scholes (1990: figure 2.1) describes the essence of cyclic illumination: 'The world interpreted in terms of ideas whose source is the world itself.' This diagram (modified in the light of Checkland and Scholes, 1990: figures 1.1 and 1.3) is reproduced as Figure 49. The ideas we have abstracted from the world influence further perception. The

ideas, in a sense, create a new perception of the world. This new perception can then lead to the abstraction of further ideas which themselves create a new perception, and so the cycle of creation and discovery continues.

Ideas abstracted from the world are not simply arbitrary or conventional. Even if sanctioned by consensus, they cannot mould the world to any form we wish. Comparing the ideas we have abstracted with future perceptions a discrepancy may be found. The error is not in the world but in our ideas about the world. These ideas must be adjusted and corrected. If this is not possible then they must be abandoned. Figure 50 (Checkland and Scholes, 1990: figure 1.3 modified in the light of figures 1.1 and 2.1) therefore more clearly expresses the empirical element of cyclic illumination.

So far no distinction has been made between public and private ideas and concepts, between objective and subjective knowledge. We have two worlds, as it were, the perceived world and the world of 'experience based knowledge' (Checkland and Scholes, 1990: 3). In the context of soft systems analysis, where Checkland and Scholes introduce these ideas, human concepts derived from the world must be taken as given. The task is then to use them constructively to alter the problem situation and modify them if necessary. In science, however, we ask for ideas and concepts that are derived by some explicit means, a methodology, that is open to public scrutiny and logical analysis (Ziman, 1968). Figure 50 may therefore be modified so as to represent science to yield Figure 51 (cf. Checkland and Scholes, 1990: figure 2.2).

Figures 52 and 53 describe cladistic analysis as a system of cyclic illumination. Figure 52A shows the derivative stage, that is character conceptualisation. Character concepts are tested against further specimens, and if found not to be applicable are modified or abandoned. Features seen in available specimens are extrapolated in the assumption that they are representative for the holomorphology of the species. Factors of ontogeny and tokogeny (e.g. differential growth, sexual dimorphism) are taken into account in this extrapolation. It can be seen that the attempt to form character concepts can result in the falsification of species concepts. Figure 52B shows how the derivative stage can feed back on the fundamental stage. Specimens supposedly of the same species may fall outside the range of variation expected for its holomorphology. Specimens supposedly of different species may fall within the range of variation expected for a single holomorphology. In other words, all differences between the two specimens from the supposedly different species can be explained as caused by the processes of ontogeny and tokogeny by which biological populations maintain themselves in nature.

Figure 53A describes the general stage, that is the use of a parsimony algorithm to generate a set of cladograms from the data available. This involves the decision that particular states comprise particular taxa. Such a decision may be checked by reexamining specimens of the species inferred to have inherited the taxon to see if the specimens exhibit the characters that comprise the taxon. This may reveal that erroneous decisions have been made for those species. Figure 53B shows that it is in assessing the results of a cladistic analysis that the general stage feeds back on the derivative stage. Two of the simplest criteria are chosen for sake of example, firstly, comparison with the worker's own intuitive assessment of the study group and secondly, comparison with the views of other workers. An initial intuition may indicate that a taxon is incorrectly placed. Attention would be directed to characters which influence the taxon's placement and these may be found to be poorly conceptualised. On the other hand the intuition may encourage a search for further characters that the supposedly related species exhibit which may then be brought to bear on the problem of its relationships. In order to deal with the challenge presented by the views of other workers, it may be possible to include their data in the analysis, or to alter conceptualisations of certain characters which they have also observed but perhaps in a better sample of taxa.

Species and general taxa

To refer to the entities discovered by cladistic analysis as 'higher taxa', 'supraspecific taxa', 'monophyletic groups', or 'historical groups' is to rely on a group concept of taxa and on the notion of focal, or hierarchical, level which that embodies. Traditionally then, general taxa are seen as groups of species, i.e. existing at a higher hierarchical level than the species. However, if a general taxon is seen as a relationship inherited by species, then the traditional descriptions are inapplicable. Species are fundamental taxa, they exist in the fundamental realm. General taxa cannot be groups of species, since general taxa and species exist in different realms. General taxa are not groups of species, they are relationships inherited by species. It follows that a cladogram, as a diagram of the pathways of morphological inheritance, is not a hierarchy of groups within groups. But such a diagram may be treated as isomorphic to a diagram of set membership, that is, to a cladogram in the sense of Nelson (1979) and Friday (1994). Here the historical meaning of the diagram is omitted, and the diagram simply represents a hierarchical classification. A phenogram may be treated as a diagram of set-membership, but is not supposed to be isomorphic to a diagram of the pathways of morphological inheritance since it does not embody a concept of taxic homology. I have suggested elsewhere (Wood, 1995), that the terms monophyletic, paraphyletic

and polyphyletic should only be applied to cladograms when they are treated as hierarchical classifications.

Nelson and Platnick (1981: 12) conclude their discussion of the nature of species with the following definition: 'the smallest detected samples of self-perpetuating organisms that have unique sets of characters.' However, this definition implies an operational method of detection and that species are the smallest groups detected by this method. However, we may ask then, what are the entities that have been analysed to arrive at this conclusion? If we say that species are the terminal entities of cladistic analysis then we enter a circular argument: this conclusion must be based on a cladistic analysis that justifies them as such. Vrana and Wheeler (1992) conclude instead that individual organisms are the terminal entities of analysis, and that a limit to resolution (at which divergent evolution is said to be replaced by reticulation) must be discovered empirically: 'Certainly it might be a consistent and useful definition if the term "species" always applied to that level below which reticulation occurred. The caveat is that there is no way to know this prior to analysis, thus in many cases applying the term by this definition must be a statement of blind faith' (Vrana and Wheeler 1992: 69). Vrana and Wheeler do not, however, address the issue of focal context. By discussing whether or not species are the smallest taxa definable (by general character states), species are treated as general taxa. The special place of species is not due to them being general taxa at the lowest possible hierarchical level. A species concept is needed in order to assess the variety of specimens needed for a representative sample of fundamental patterns. And no fundamental patterns, no general pattern. No species, no cladistic analysis.

Nixon and Wheeler (1990) agree with me: 'In addition to the traditional roles of describing, naming, and classifying the kinds of living things, systematists also must recognise the biological entities that can be analysed using cladistics' (p. 213). They advocate a 'phylogenetic' species concept, after Cracraft (1983), that can be implemented prior to cladistic analysis (p. 217). Nixon and Wheeler give the following definition: 'the smallest aggregate of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)' (p. 218). The use of epithet 'phylogenetic' is rather puzzling here, since their concept of 'population' is based on 'genealogical (not phylogenetic) relationships of its component individuals' (pp. 218-219). Awkward cases, where individuals lack the characteristics of their species, can be resolved by observing the genealogies of these individuals directly: 'Such individuals probably would not be identifiable as members of the species except by direct association with other individuals of the species that bear diagnostic characters. The (comparable) offspring of such individuals would bear the diagnostic characters of the species, indicating that the

parents did not lack the characters of the species' (p. 219). Genealogy is indeed a process by which biological populations maintain themselves in nature. If directly observable genealogical relationships may indeed aid in the assignment of individual organisms to species. I suggest that we may use our knowledge of the characteristic effects of particular biological processes in assigning organisms to species, even if those processes may not be directly observable in the species we are dealing with. For example, Merrett and Marshall (1981) were led to synonymise two species of the deep sea fish genus *Coryphaenoides*, namely *C. colon* and *C. zaniophorus*. The two species were found at the same capture station. Smaller individuals were found to have the characteristic proportions of *C. zaniophorus* and the larger individuals the characteristic proportions of *C. colon*. They conclude that the differences between the two are explicable as allometric variation within a single species. Given the recognised phenomenon of allometric growth, the combinations of character states found in *C. colon* and *C. zaniophorus* fall within the range expected for the holomorphology of a single species.

3.3.4: Stability and Constraint

The theme of stability is common to all the ground-breaking accounts of hierarchy theory. The parable of the two watchmakers, first presented by Simon (1962: 470), provides a clear statement of this theme and has been variously adapted by Koestler (1967: 45-47) and Allen and Starr (1982: 49-51). Simon describes two watchmakers, named Hora and Tempus (Koestler renames them Bios and Mekhos, and Allen and Starr provide a factual analogue of the fictional Hora). Both Hora and Tempus make watches that consist of 1000 parts. However, Hora manufactures his watches in subassemblies of 10 parts each, whereas Tempus assembles his watches part after part. The subassemblies that Hora has discovered are *stable*. They do not fall apart when Hora leaves them to cope with disturbances, such as the telephone ringing. But for Tempus only the completed watch is stable. A disruption at any stage except the final one requires him to start from scratch again. Hora's strategy is superior for dealing with environmental disturbances, caused by customers ringing the workshop, since the use of stable subassemblies minimises the effect of those disturbances. Watches built by Hora as a hierarchy of subassemblies will come to predominate in the market at the expense of the watches of Tempus.

Simon (1962) draws two conclusions from his watchmaker parable, in order to emphasise the importance of hierarchical structure. Similar conclusions are reached by Dawkins (1976, 1989a,b). Through his popular writings Dawkins has gained something of a reputation as a reductionist and arch-adaptationist. He has advocated the gene not the individual as the level of selection (Dawkins, 1982, 1989b) and natural selection as the creative force in evolution (Dawkins, 1986). It may then seem strange to find that he has adopted some of the language, and the conclusions, of hierarchy theory.

(1) In nature only the stable survive. Survival of the stable is a generalisation of survival of the fittest (Simon, 1962: 471). Thus, the rule of the survival of the stable extends into the inanimate, as well as to animate (Simon, 1962: 479).

'Darwin's "survival of the fittest" is really a special case of a more general law of *survival of the stable*. The universe is populated by stable things. A stable thing is a collection of atoms that is permanent enough or common enough to deserve a name ... The things that we see around us, and which we think of as needing explanation - rocks, galaxies, ocean waves - are all, to a greater or lesser degree, stable patterns of atoms' (Dawkins, 1989b: 12). 'The earliest form of natural

selection was simply a selection of stable forms and a rejection of unstable ones' (Dawkins, 1989b: 13).

(2) 'Among possible complex forms, hierarchies are the ones that have time to evolve' (Simon, 1962: 473).

Dawkins (1976) discusses Simon's argument in the context of a hierarchical approach to animal behaviour and suggests that it also applies to the nervous system. He summarises Simon's principle as follows: 'that the evolution of statistically "improbable assemblies proceeds more rapidly if there is a succession of intermediate stable subassemblies. Since the argument can be applied to each subassembly, it follows that highly complex systems which exist in the world are likely to have a hierarchical architecture"' (Dawkins, 1976: 16; Dawkins, 1982: 251).

Dawkins (1989b) points out, however, that we cannot expect complex organisms to arise through the simple heat agitation processes that brought about the stable inanimate forms (Dawkins, 1989b: 14). What is required are special molecules, called *replicators*, which are able to hold information and pass it on to future generations. Selection then accumulates beneficial modifications and complex forms are built up. Elsewhere he provides a second condition: 'It is that there must be an embryology; the genes must influence the development of a phenotype; and the replicators must be able to wield some phenotypic power over their world, such that some of them are more successful at replicating themselves than others' (Dawkins, 1989a: 202).

We may reflect on these two requirements by considering how we might go about defining a living organism. Cairns-Smith (1982) divides definitions of life into two classes: genetic and teleonomic. Genetic definitions concern the properties of organisms that we would expect as prerequisites for an evolutionary process, namely some sort of replicating molecule that can act as a hereditary material. Teleonomic definitions concentrate on the products of evolution, namely elaborately integrated wholes, apparently contrived, exhibiting a high degree of cooperation between their parts. Cairns-Smith shows that it is the definition of Waddington (1968: 3) that provides the link between these two classes of definition: living things take part in the long-term processes of evolution. Thus organisms that are beyond the ability to reproduce are products of the long-term processes of evolution, although no longer active participants. The very first organisms on earth are at the beginning of those long-term processes, although not yet possessing the high degree of apparent design typical of later forms.

The genetic and teleonomic definitions of life relate to the dual aspect of every organism. The hereditary material embodies the organism's genotype, the messages replicated from generation to generation. The organism's subtly cooperating parts are its phenotype. Organisms generate more organisms of like kind and set up cycles of self-generation. Heritable variation results from imperfections in the replication of genetic information. Changes accumulate in the genotype, which in turn manifest themselves in the phenotype of the organism. The cycles of self-generation thus have a direction, a history, as a result of these accumulated changes. Descent with modification thus requires a logical separation of genotype and phenotype: a genotype to perpetuate change, a phenotype to manifest it.

Dawkins (1989a) provides an insight into the nature of development through an elaborate thought experiment, aided by a computer program. He is interested in creating 'biomorphs', two dimensional images that evolve according to the two conditions he has outlined above. The phenotype of each biomorph consists of a pattern of pixels on a computer screen. What is the best way to organise the genome that codes for this phenotype? The first idea that suggests itself is to have a gene coding for each pixel: 85,000 genes for each pixel on the Macintosh screen. Any pattern of pixels, any conceivable biomorph, could in theory be generated through gradual change at the level of both the genes and the overall morphology. 'But only in theory. In practice we'd be waiting till kingdom come ... Our improvements [to the developmental program] will take the form of constraints. Constrained embryologies are improvements over naive pixel-peppering, not because they have greater generality but because they have less. Naive pixel-peppering can produce all possible pictures, including the set that anyone might regard as biological. The problem lies in the astronomical number of nonsense pictures that it can also produce. Constrained embryologies have a restricted set of phenotypes that they can generate, and they will be specified by a smaller set of genes, each gene controlling a more powerful drawing operation than colouring a single pixel' (Dawkins, 1989a: 204-205).

Dawkins (1989a) has realised that, for complex forms to evolve, not only must there be replicators, but the developmental system must be set up in a certain way, specifically, so that it embodies particular *constraints*. The existence of a characteristic set of developmental constraints has the negative result that evolution is canalised along certain pathways. Dawkins shows how he tried to select biomorphs that corresponded to letters of the alphabet, specifically to be able to spell his name in biomorph characters. However, he was unable to generate a 'K' despite all his efforts and he could not remove a tail from the rather triangular 'D' (Dawkins, 1989a: 216).

The conclusions that Dawkins has made on the nature of the developmental system match those arrived at empirically by Goldschmidt (1938, 1940). There is no great divide between their views as you might expect (see Gould, 1980c, on the rehabilitation of Goldschmidt). I identify three points of correspondence between Dawkins and Goldschmidt:

(1) Genetic change causes local changes in the partial processes of development (Goldschmidt, 1938: 51-52; see also Alberch, 1982: 326)

'Genes don't control small fragments of the body, the equivalent of pixels. Genes control growing rules, developmental processes, and embryological algorithms. Powerful though they are, an important feature of these growing rules is that they are local. There is no grand blueprint for the whole and when all the local instructions are obeyed together a body eventually results' (Dawkins, 1989a: 206).

(2) Small genetic changes accumulate until a threshold is reached and great potential for rapid macroevolution is released (Goldschmidt, 1940: 396)

Dawkins (1989a) proposes modifications to his basic developmental program. These involve the introduction of a number of genes that regulate the kind of patterns that can be produced. Thus there are genes for various patterns of symmetry or segmentation. These modifications lead to 'opulent flowerings of new emergent properties' defining 'a whole new range of types' (Dawkins, 1989a: 209, 212). Here Dawkins has introduced genes for global patterns. But given his statement in (1) perhaps it is not too much to imagine that these global patterns might in fact be the result of the local interactions as Goldschmidt envisaged.

(3) Hopeful monsters (Goldschmidt, 1940: 390-393)

'I suspect that the first segmented animal was not a dramatically successful individual. It was a freak, with a double (or multiple) body where its parents had a single body. Its parents' single body plan at least fairly well adapted to the species' way of life; otherwise they would not have been parents. It is not, on the face of it, likely that a double body would have been better adapted. Quite the contrary. Nevertheless, it survived (we know this because its segmented descendants are still around), if only (this, of course, is conjecture) by the skin of its teeth' (Dawkins, 1989a: 218). This seems a bizarre scenario, and one that appears to contain a dangerous element of circularity. We reconstruct a hopeful segmented monster to explain the existence of segmented animals and justify that, however unlikely it was, it survived because we have segmented animals here today. The standard objection is that a single monstrous individual is produced easily enough, but how do we arrive at an interbreeding population of monstrosities? Dawkins and Goldschmidt have

emphasised the potential of the developmental system to produce sharply discontinuous changes to such an extent that they have brought their theory of macro-evolutionary change to brink of non-Darwinian saltationism.

However, neither Dawkins nor Goldschmidt need do so. An alternative course is provided by their own observations: 'Suppose that a discontinuous change in adult form arises from a small genetic alteration. Problems of discordance with other members of the species do not arise, and the large, favourable variant can spread through a population in Darwinian fashion' (Gould, 1980c: 191). Gould suggests that the large change in morphology may cause a cascade of related adaptations. A new mode of life will then be opened up through a series of gradual modifications.

Stability and homology

'The most fundamental principle of evolutionary strategy, related to the watchmakers' parable, is the *standardisation* of subassemblies ... Animals and plants are made out of homologous organelles like the mitochondria, homologous organs like the gills and lungs, homologous limbs such as arms and wings. They are the stable holons in the evolutionary flux' (Koestler, 1967: 135, 139). Riedl, in the following passage, reflects similarly on the stability of homologues: 'Actually, every homologue is characterised by the fact that it shows adaptive freedom in only a few directions, but fixation in many others. If this were different, if every character were free to change in every direction, the living world would appear as a random chaotic mixture of patterns, as chaos, and the single relationship left among representatives would not relate to common ancestry but only to common functions, such as analogous limbs, horns, wings, jaws, and so forth' (Riedl, 1977: 354; cf. Alberch, 1982: 315-316). Riedl therefore introduces a concept of morphological stability, or fixation, to account for the fact of homology. Parts of organisms possess a stability which permits us to recognise relationships between them that are not the result of shared function. But stability is also the ability 'to adapt in response to shocks from the environment' (Checkland and Scholes, 1990: 19). Morphological stability is thus adaptability, or *evolvability* (cf. Waddington, 1957: Chapter 5). Dawkins (1989a) defines evolvability as follows: 'New embryologies that are evolutionarily fertile tend to be the embryologies that characterise the forms of life that we actually see. As the ages go by, changes in embryology that increase evolutionary richness tend to be self-perpetuating. Notice that this is not the same thing as saying that embryologies that give rise to good, healthy individual organisms tend to be embryologies that are still with us, although that, too,

is no doubt true. I am talking about a kind of higher-level selection, a selection not for survivability but for evolvability' (Dawkins, 1989a: 218). The stable morphologies that we see today are the product of embryologies that were pregnant with evolutionary potential. A stable morphology, although the result of a constrained embryology, shows great evolutionary potential in the few directions open to it.

To sum up, we are apparently provided with two ways of describing the stability of the organism: (1) the organism consists of stable subassemblies, or homologues; (2) the organism's development is set up so that it embodies particular constraints, homologies. However, it is not parts of organisms (homologues) that are inherited from generation to generation. That would imply a material continuity possible only for the genotype. What are conserved through phenotype after phenotype are relationships of constraint (homologies). The inheritance of these relationships from generation to generation maintains the organism as a set of stable subassemblies. The organism's developmental constraints filter out the effects of destabilising genetic mutations, but at the same time make the organism adaptable to future environmental changes.

Hierarchies of constraint

'Hierarchies can be profitably viewed as systems of constraint' (Allen and Starr, 1982: 11). Allen and Starr (1982) discuss constraint in terms of information flow through the hierarchy. They adopt Koestler's metaphor of Janus (Koestler, 1967: 47-49). In the Roman mythology the god Janus had two faces; the Latin for door *ianua* is from the same root. Each holon is thus a doorway through which information enters and departs, flowing down the hierarchy from the environment and flowing up from lower levels of the hierarchy (Allen and Starr, 1982: 9). The position of the holon in the hierarchy is determined by the way in which the holon filters information that it receives. The asymmetry of information exchange produces relations of constraint between holons. Constraining holons filter out the signal that they receive from constrained holons and remain largely unaffected. Constrained holons receive the signal from constraining holons relatively unfiltered and thus are significantly affected. (This account of constraint and information exchange is derived from Allen and Starr, 1982: 20; cf. Dawkins, 1976: 14).

Signals pass out from the genome and modify the environment to produce the phenotype. This is what we call development. Development is an interaction between the genetic signals and the

environment. The dividing line between the phenotype and the environment is not precise: the phenotype 'is a bit of the environment locally modified by the genetic information' (Cairns-Smith, 1982: 80). It is possible to imagine that the phenotype, the manifestation of the effects of the genetic signals, extends into the environment beyond the bounds of the body housing the corresponding genes. This is the essence of Dawkins' idea of the 'extended phenotype' (Dawkins, 1982).

We can envisage the phenotype itself as a set of holons which differ in the extent to which they filter genetic signals as they pass out into the environment. Phenotypic holons that exert little constraint on the genome express the genetic signal relatively unfiltered. Phenotypic holons that exert heavy constraint on the genome express the genetic signal significantly filtered. Thus continuous genetic differences between organisms in a population may be expressed as continuous phenotypic differences, if the corresponding genetic signals are relatively unfiltered, or as discontinuities, if the genetic signals are significantly filtered. The accumulation of genetic changes will cause gradual modifications of the phenotype in the first case, but sudden shifts between stable states in the second. In this way phenotypic holons can be said to constrain the dynamics of genetic change. These constraints are properties of the developmental system: they are *developmental constraints*. Genetic signal is filtered in such a way that across individuals, and indeed across species, qualitatively different morphologies are produced. (An understanding of the developmental system in terms of its inherent constraints cannot be derived from the study of a single individual; *contra* Dawkins [1989a: 203].)

If holons are doorways then information passes through them in two directions. If we believe that development is the result of genetic information passing out through a hierarchy of holons into the environment, then there must be a process in which genetic information flows back the other way. I suggest that information flows back from the environment to the genome when organisms reproduce. On their return journey genetic signals pass through a hierarchy of *adaptive constraints*. The position of a phenotypic feature in this hierarchy is determined by the selective or adaptive advantage of that feature. As in the case of development we must think not about a single individual, but a set of individuals, in this case the population. Selective filtering occurs when the population reproduces as a whole to provide the next generation. The predominance of a gene in the next generation is proportional to the strength of the signal arriving from the environment back in the communal genome, or gene pool. Adaptive, i.e. selectively advantageous features amplify the signal, whereas maladaptive features attenuate it. A particular phenotypic feature may filter the signal of many genes. It is also possible that selective filtering of different features is correlated in

some way. There is no need to conceive a simple relation between genetic signal and selective constraint. It is on genetic signals that selection acts: genetic signals are selectively filtered. This is the essence of another of Dawkins' ideas: the 'selfish gene' (Dawkins, 1989b). Dawkins has been dubbed a reductionist for advocating the gene as the level at which selection acts. I have shown here that his position is exactly that expected from hierarchy theory.

Homologies are rules of interpretation that make the phenotypes of organisms meaningful. Homologies are developmental constraints conserved among organisms. Homologies are the rules operating at the phenotypic level that constrain the dynamics of the genetic level (cf. Allen and Starr, 1982: 42). Through descent with modification then, organisms accumulate inherited constraints on their genetic dynamics, or as Riedl (1977) would put it, on their adaptive freedom. The type is the totality of constraints inherited by the organism. The homologies, the parts of the type, are the individual constraints inherited by the parts of the organism. A general taxon or type characterises 'a set of species sharing a common pattern of constraints and adaptive opportunities ... the key event in the origin of a [general] taxon is a change in the pattern of constraints' (Wagner, 1986: 154-155).

I have described above a 'feedback regulatory cycle' operating between genotype and phenotype, similar to that envisaged by Riedl (1977). In order to explain the stability of homologues over evolutionary time, Riedl saw the necessity of 'feedback loops of cause and effect both from the genome to the phenome and in the *reverse* direction' (Riedl, 1977: 364). This sounds rather puzzling but can be understood in terms of the expectations of hierarchy theory. The dynamics of gene frequencies may be the cause of phenotypic change, but the effects are constrained by the phenotype itself. Thus information flows both ways: from genotype to phenotype in the causal relationship enshrined in the 'central dogma' of molecular biology, and from phenotype to genotype as constraints enshrined in the systems approach (Riedl, 1977; Wagner, 1986). I might even suggest that Riedl's notion of burden, or systemic position, is equivalent to the position in the hierarchy of constraint. Structures of high burden have great stability and are unlikely to be rejected or modified by natural selection (Riedl, 1978: 239).

Dynamical systems theory

Like Dawkins (1989a), Alberch (1982) describes the idea of developmental constraints with the aid of a thought experiment. Consider, for sake of example, that the whole diversity of a phenotype can be expressed in terms of two variables, x and y. The distribution of forms found in nature is not continuous. Instead, phenotypes cluster and certain regions of the xy space remain empty. Now let us take a population of one of the natural forms and breed the population for a large number of generations. The effect of natural selection is eliminated as far as possible, by enforcing random mating and minimising competition. The overall genetic variability of the population can also be increased through the use of mutagens. Score all the new phenotypes in terms of x and y, including teratologies. We will get the same phenotype clusters as before, plus new ones, which will be naturally lethal or non-functional phenotypes. 'However, there will still be states that are prohibited by developmental constraints' (Alberch, 1982: 318). The basic effect of developmental constraints on the apportionment of morphological variation is that 'a continuous distribution of genotypes can result in a discontinuous distribution of phenotypes' (Alberch, 1982: 319).

The theoretical framework that Alberch (1982) provides for understanding developmental constraints is dynamical systems theory: 'Developmental systems are complex non-linear dynamical systems. It is an intrinsic property of such systems that they will fall into a discrete number of stable states, i.e. we should find a discrete and bounded distribution of phenotypes. Furthermore, non-linear dynamical systems will exhibit preferred transitions of form' (Alberch, 1982: 327-328). The analysis of development as a dynamical system enables possible stable states of morphology to be identified and also the preferred transformations between those states. The morphogenetic process is conceived as a set of simple, locally-acting "assembly" rules (Alberch, 1982: 321). Genetic change perturbs the parameters of the developmental system, but as long as the parameters stay within certain limits, the morphology remains unchanged. The morphology is said to be self-regulating or canalised (Waddington, 1957). However, if a particular parameter reaches a threshold value then a sudden shift to a different stable state occurs. This effect is known in the language of dynamical systems theory as 'bifurcation'. The parameter space for a particular dynamical system is said to have 'bifurcation boundaries' at which the global behaviour of the system, such as the resulting morphology, shifts from one stable state to another. Oster and Alberch (1982) describe 'how the bifurcations in the developmental program acts as a *filter*, giving order to the random mutations in the genome, so as to present natural selection with a small subset of the possible phenotypes' (Oster and Alberch, 1982: figure 11, legend; my italics). Thus

developmental bifurcations 'filter random mutations, giving them a non-random character' (Oster and Alberch, 1982: 454).

The view of the developmental process derived from the theory of non-linear dynamical systems is compatible with that provided by hierarchy theory. In fact, they complement each other. On the phenomenological level, the notion of developmental constraints is left obscure by dynamical systems theory. A phenotype can never be expressed in terms of just two variables. Hierarchy theory, as applied to systematics, clarifies the notion. Homologies are developmental constraints and, through descent with modification, are inherited by parts of organisms. Dynamical systems theory provides the basis of constraint at a deeper level. Developmental bifurcations filter genetic signals, producing variation at the morphological level which is constrained or canalised into particular stable states.

Quantity to quality

Gould (1980b) provides a lucid description of the two proposed modes of macroevolutionary change: gradualism and punctuated equilibria. Gradualism asserts that evolution proceeds by the continuous, gradual change at both the level of the gene and the total morphology. The theory of punctuated equilibria (Eldredge and Gould, 1972; Gould and Eldredge, 1977) asserts that species appear rapidly and then remain stable for the rest of their history. Gradualism is forced to explain the existence of discontinuities in nature as gaps in the preservation of the fossil record. Punctuationism, on the other hand, sees the gaps as real, to be expected by the theory. The theory explains discontinuity in terms of a process of speciation which requires rapid change in both genotype and phenotype in a small population (Gould, 1980b: 183).

The theme of Gould (1980b) is that gradualism has found favour because of the Western preference for slow, orderly transformation. A preference for revolutionary, cataclysmic change belongs to a different tradition, namely the tradition of dialectics derived by Engels from Hegel's philosophy: 'The dialectical laws are explicitly punctuational. They speak, for example, of the "transformation of quantity into quality." This may sound like mumbo–jumbo, but it suggests that change occurs in leaps following a slow accumulation of stresses that a system resists until it reaches the breaking point' (Gould, 1980b: 184–185). I argue that the concept of a "transformation of quantity into quality" offers an explanation of the existence of

discontinuities in nature which does not require reference to a separate macroevolutionary theory. *Quantitative change at the genetic level gives rise to qualitative change at the morphological level.* Change at the level of the genome may be continuous, but discontinuous at the level of the overall form. If some phenotypic characters do change continuously it is because the corresponding genetic signals are expressed relatively unfiltered. It is these characters that have been studied in genetic experiments that have supposedly demonstrated evolution to be change in gene frequencies. The properties of the developmental system are such that genetic changes, even if copious, small and undirected, can still give rise to specific, large, directed changes of form: 'These [small, genetic] changes can have substantial impact on adult phenotypes because they operate by altering rates of development early in ontogeny, with cascading effects throughout later growth' (Gould, 1980a: 45).

3.3.5: A biological principle of complementarity

Organisms and species comprise aspects of both genotype and phenotype: genome or gene pool and holomorphology respectively. Phylogenetic history can be described as the history of the genotype and the history of the phenotype. There are therefore two different ways of approaching the phylogenetic history of organisms and species, genetic and morphological. The genetic approach takes DNA sequences as the source of its data, since these comprise the genotypic information passed on from generation to generation. All aspects of the phenotype provide the source of data for the morphological approach.

DNA sequences, as genotype, have no ontogeny and exist effectively in only one dimension (Patterson, 1988a: 74; 1988b: 610). Ontogeny is the process by which the information stored as the genotype is translated into the three-dimensional structure of the phenotype (Patterson, 1988a: 94). The genotype can be expressed in simple physical and chemical terms. This is what a nucleotide sequence is. The phenotype cannot be reduced to a physicochemical description if essentials are not to be lost. Its hierarchical organisation has emergent properties, homologies, which are irreducible to the underlying physics and chemistry.

Tennant (1986) provides an interesting discussion of how it might be possible to define a morphological homology like the gastrula. Is it possible to reduce the homology to a precise definition in physical and chemical terms? We might start by defining the gastrula as certain types

of cells in particular topological configurations. A gastrula is thus a hollow ball of cells, where the outer layer of cells is ciliated and the inner layer is unciliated and free to divide. However, in a purely reductionist exercise each cell would have to be described in terms of particular configurations of nuclear, cytoplasmic and membranous components. Each of these components could be reduced to configurations of different sorts of molecules, and so on *ad infinitum*. We might take a different approach and describe the gastrula of each species in terms of its characteristic cell types, and the characteristic rate at which these differentiate. But even with this approach, the term would become complicated and unwieldy. Moreover, the term would lose what Tennant calls its 'open-textured meaning'. A student is taught to recognise a gastrula by being shown an example, probably together with a simple diagram. The student is able to grasp the concept intuitively. Equipped with this knowledge, he is able to apply it even to a previously undescribed species. Any description of the gastrula purely in physical and chemical terms would have to be altered with the discovery of the new example. However, the term itself would survive this extension unchanged. It is Tennant's belief that ultimately morphological homologies will submit to the reductionist exercise. But I think his claim misses the point. The beauty of morphological terms lies in their openness, and the problem with attempts to reduce them is that this openness is lost. The use of character concepts which are open and irreducible characterises the intuitive ability for *pattern recognition* possessed by human beings (see Ziman, 1978). The formulation, learning and application of the concept 'gastrula' all necessarily involve human observers. For this reason morphological characters are observer-dependent or intersubjective: they express knowledge which 'can only be validated and translated into action by the intervention of human minds' (Ziman, 1978: 7).

An analogous process of pattern recognition to that involved in morphological work might well be employed in the generation of nucleotide sequence data. Sequences may be simply aligned by eye, gaps being inserted by inspection to produce the closest visual match between the sequences. But again we may ask, is it possible to replace this intuitive process with a mathematical algorithm embodied in a computer program? Strikingly this problem has been solved by Bishop and Thompson (1986). They were able to carry out alignment of pairs of sequences under a model of evolution that incorporated substitution, deletion and insertion events. The achievement of Bishop and Thompson is of great theoretical importance, even though it is practically limited. It shows that genetic data is fundamentally different from morphological data. Patterson (1988b) discusses the attempts made by Jardine and Jardine (1967) to develop a mathematical means of comparing morphologies. He notes significantly that the computer program they wrote was quickly seen to be 'only an aid' (Jardine, 1970: 332). Patterson links the failure of their attempt to the fact that

morphology exists in three dimensions, rather than one. We may link it to the fact that, unlike DNA sequences, morphologies are hierarchically organised.

The genetic approach deals with linear DNA sequences, which are aligned according to a dynamical model of the causal process of evolution, a process assumed to take place independent of the observer. The context of morphology, with its inherent hierarchical organisation, dictates that character concepts are the result of the interpretations made by a community of observers. The morphological approach derives its data through a process of interpretation, similar to that involved in any linguistic communication. Morphological comparisons are governed by a creation/discovery procedure and therefore require an observer. What is important is the code, the means by which we bring meaning to the study group, in terms of meaningful features (similarities) and meaningful similarities (homologies). The code therefore consists of rules for the interpretation of the structures of the study group. What are we to make of the existence of two such different approaches to systematics? Are we to say that one must be more reliable than the other? A principle of complementarity, on the other hand, would argue for 'the necessity of formal incompatibilities in the dual modes of description, in contrast to the unity and consistency of the classical paradigm of a unified formalism' (Pattee, 1978: 193). A concept of complementarity has been introduced into systematics by Rieppel (1987, 1988b). 'Neither perspective is in itself sufficient to produce a complete explanation of natural phenomena, nor is it possible to reduce one perspective to the other. Observation and explanation may proceed from either point of view, resulting in different appearances subject to alternative explanatory theories. There result alternative and complementary views of a whole which as such remains incomprehensible' (Rieppel, 1988b: 5). Pattee (1978) and Allen and Starr (1982) discuss three heuristic criteria designed to identify instances of true complementarity between two modes of description. I shall show below that each identifies a complementarity between the genetic and morphological approaches to systematics. This conclusion bears out the suggestion made by Pattee (1978: 195) that the basis of a principle of complementarity for biology rests on the distinction between genotype and phenotype.

(1) Structure versus function, laws versus rules (Pattee, 1978: 195-196)

Pattee illustrates the complementarity existing between structure and function using the example of the genetic code. The structure of the DNA can be understood in terms of physical *laws*, whereas its function can only be comprehended in terms of *rules* of interpretation specific to living organisms. The coding relationship between DNA triplet and aminoacid is not reducible to physical laws, but rather to be understood as a property of the whole organism. The two

approaches to systematics we have discussed are readily understood in these terms. The genetic approach assumes a process of evolution that, at least for the purpose of the analysis, lawfully governs all sequence alignments over the whole study group. The aim of the approach is to improve the fit between the model and the data. The aim of the morphological approach is to discover rules for the interpretation of biological structure. Thus the underlying aims of the two approaches can be seen to have the character of law or rule respectively. The two approaches are therefore complementary.

(2) Rate-dependent versus rate-independent, dynamic versus linguistic descriptions (Pattee, 1978: 195)

The genetic approach generates its data through the use of a dynamical, necessarily rate-dependent model of evolution. The morphological approach derives its data through a process of interpretation and the results of the interpretation are independent of the rate at which the interpretation is carried out.

(3) Observer-independent versus observer-dependent (Allen and Starr, 1982: 43)

In the genetic approach the alignment of sequences can be carried out effectively independent of the observer. In the morphological approach the formulation of characters inevitably involves the observer's judgment.

Models of change

Statistical methods, which adopt some stochastic model of the evolutionary process, are commonly employed for nucleotide sequences, whereas the cladistic method has been widely used to analyse morphological data. The details of different parsimony methods are provided by Kitching (1992). Kitching also describes the method of generalised parsimony (see Swofford and Olsen, 1990: 463-465; Swofford, 1991: 15-17; Kitching, 1992: 55-58; also Williams, 1992: 115-119). Here a 'cost' is assigned to each transformation between states. The costs are represented as a square m-by-m matrix, in which the elements, S_{ij}, represent the increase in the length of the cladogram that is associated with the transformation from state *i* to state *j*. The value m is the total number of states for the character. Any assumptions about order and weighting, any conceivable character coding in other words, can be incorporated into the appropriate cost matrix. For instance, transformations deemed to be impossible can be given a cost of infinity. Note that in generalised parsimony each character state change has a particular weight associated with it. Parsimony as a general method of placing character states on a cladogram specifies the estimate of the true cladogram as the solution of minimal cost. Each parsimony method has its characteristic cost matrix (see Kitching, 1992: Table 4.1). The specific cost matrix is the model of the evolutionary process assumed by the particular parsimony technique.

Mickevich and Weller (1990) make a distinction between transmodal characters and cladogram characters. Transmodal characters they define as based on some evolutionary model, whereas cladogram characters are supposedly model-free, based only on the hierarchy of the cladogram. Buckup (1991) shows, however, that cladogram characters are, indeed, transmodal. Mickevich and Weller's intention is to devise a method of character coding that is independent of assumptions about evolution, in the words of Platnick (1989), 'a method that would allow attributes of the data themselves to determine the ordering...' (p. 23). However, since all characters are transmodal, any method of coding makes more or less explicit assumptions about the evolutionary process.

The assigned weights reflect our assumptions about which state changes are particularly favoured. It is readily apparent, from the language that we use for morphology, that the model of evolution employed in cladistics is deterministic, rather than stochastic (Bishop and Friday, 1985). Indeed, Friday makes the point that stochastic models are unable to deal directly with natural selection, usually characterised as a deterministic force (Friday, 1989: 232; 1994: 211). However,

deterministic models deal only with (favoured or unfavoured) directions of change, and thus information about evolutionary rates is lost.

Deterministic and stochastic models are complementary following the criterion developed by Allen and Starr: 'It is worthwhile not only to identify what the two complements achieve, but also to identify what is sacrificed, what is the price paid for the perfect internal consistency of each mode of description (Allen and Starr, 1982: 62). Information about the forces of natural selection and developmental canalisation are incorporated into deterministic models, but are not explicitly described by stochastic models. Information about the rates of evolution taking place in time are incorporated into stochastic models, but are foreign to deterministic models.

Cladograms and family trees

The results of the morphological approach to phylogenetic reconstruction are cladograms in the sense of Nelson (1989). As hierarchies of types (Rieppel, 1985) cladograms have no time axis (they are rate-independent) and have no notion of ancestry (instead, inheritance). Taxa revealed through cladistic analysis are not groups consisting of an ancestral species and its descendant species; taxa are relationships inherited by species. Cladograms do not characterise biological species; they are diagrams which summarise relationships of species. A family tree, on the other hand, is 'a simple model of the pathways of genetic transmission' (Bishop and Friday, 1985: 273). A family tree describes the fate (change without splitting, splitting, extinction) of replicator-continua (Lidén, 1990: 184). If the replicators involved are gene pools, as they must be if the organisms being studied reproduce sexually, then the family tree describes the fate of species in their genetic aspect. Gene pool continuity is the material, biological, causal relationship that binds together an ancestral species and its descendant species (cf. Beckner, 1959: 67-68). The tree has concepts of time, ancestry and species which the cladogram lacks. These differences form the basis of the cladogram/tree distinction discovered by Nelson (1976, draft; published in Nelson and Platnick, 1981).

In the genetic approach what really matters are the nucleotide sequences and the tree of highest likelihood. Ideally there is no intermediate stage. The alignment of the sequences should be carried out as an integral part of the phylogenetic analysis. In the morphological approach what is of interest is the code, the set of patterns of constraint (derivative patterns) and the congruence among those patterns, which specifies the hierarchy of homologies (general pattern). The code brings

meaning to the multiplicity of fundamental patterns displayed by the species of the study group. In cladistic analysis we move through different focal contexts, and the contrast between derivative and general stages is much more relevant here. In the statistical approach we simply move from the lowest focal level to higher levels, from species to monophyletic groups of species. The statistical approach operates within the fundamental realm, whereas cladistics moves from the fundamental realm to the general. Conventional concepts of species and higher taxa apply only to the fundamental realm, to family trees. Species and monophyletic groups of species are fundamental taxa. They are individuals, irreproducible wholes united by gene pool continuity among their parts (cf. de Queiroz and Donoghue, 1988; Lidén, 1990). Cladograms, which describe the hierarchy of constraints inherited by species, exist in the general realm.

Pattern cladistics

Pattern cladistics (see Patterson, 1988a, for a review) may be seen to have arisen from the mistaken assumption that if cladograms are not family trees then they are not historical. Cladograms and trees are both based on evolutionary models, but models of fundamentally different kinds (deterministic versus stochastic, direction versus rate). A cladogram, although it does not rely on any concept of time or any concept of ancestry, provides a reconstruction of the total evolution of morphological characters. Many expressions of the distinction between cladogram and family tree have appeared in the literature. I suggest in each case, the suggested contrasts are imperfect representations of the complementarity that exists between linguistic and dynamic descriptions of the phylogenetic hierarchy.

1. Rieppel (1985) emphasises the contrast in terms of time-dependence by relating the cladogram to Plato's world of being and the family tree to the world of becoming. The world of being stands ideal and immutable, outside causality and outside the contingencies of time and space. Certainly this captures the nature of the cladogram as atemporal, but the other claims may be overstated. Rieppel (1992) emphasises that the cladogram describes ultimate causality, in terms of history, not proximate causality, for example in terms of developmental mechanisms. Rieppel is here emphasising that the cladogram does not lie outside the confines of causality. Describing the cladogram as 'ideal' brings in misleading connotations. This criticism might be made of the description of general taxa as types. However, Patterson (1982) makes a distinction between morphotype and archetype, morphotype being an empirical concept relating

to cladistics and archetype being the idealistic concept relating to pre-evolutionary morphology. We see that Rieppel (1985) describes the cladogram as ideal, whereas Patterson (1982) does not. As they disagree as to which is best described as ideal I would suggest that the term is best avoided.

2. Rieppel (1985) emphasises the contrast between continuity and discontinuity, and this better captures the distinction between cladogram and family tree. The pathway of genetic information, described by the tree of life, runs continuously through the hierarchy of constraints of every living organism, which is described by the cladogram, the hierarchy of life.

3. Rieppel (1991) emphasises the contrast in terms of observer-dependence by drawing on Popper's (1972) philosophy of three worlds. 'World 1' is the physical world, 'World 2' the world of our conscious experiences, and 'World 3' consists of the logical content of our theories, conjectures, guesses etc. (Popper, 1972: 73-74). Rieppel claims that the cladogram deals only with human conjectures, and thus is World 3, whereas the family tree is World 1. However, the hypothesised family tree is as much a 'theory, conjecture, or guess' as the hypothesised cladogram. If we wish to speak in Popper's terms, I suggest that cladogram and tree belongs to different realms, fundamental and general, of World 3.

4. A number of authors distinguish between cladogram and family tree in terms of pattern and process, or systematics and evolution (Eldredge and Cracraft, 1980; Nelson and Platnick, 1981, 1984; Patterson, 1988a; Rieppel, 1988b). Systematics, synonymised with cladistic analysis, is assumed to discover the pattern of 'order in nature', or 'nature's hierarchy', by a means assuming little or no knowledge of the evolutionary process. Details of the process are to be extracted from the analysis of pattern. But how if details of the evolutionary process are not built into the detection of pattern can they then be extracted? De Queiroz (1985) argues that, within a Popperian perspective, any attempt to generalise a theory of evolution from systematics involves faulty logic: Popper (1959) shows the impossibility of induction, of inferring a general theory from specific observations. Instead I suggest that cladograms and family trees are patterns of relationship reconstructed by appropriate methods of phylogenetic systematics, which adopt appropriate, but distinct, evolutionary models.

5. Brady (1985) and Panchen (1992) have taken the view that the classifications provided by cladistic analysis are to be explained by evolution as family trees. Classification is considered logically, as well as historically prior to the theory of evolution. However, we have seen how

cladograms and family trees are complementary descriptions of evolutionary history, belonging to different realms. One cannot be converted to the other, although because they both refer to the same reality, the topology of one has certain implications for the topology of the other. The series of papers from the 1970s (e.g. Cracraft, 1974; Harper, 1976; Platnick, 1977b; Wiley, 1979), supposedly describing the conversion of cladograms to trees, can only make clear these logical implications. They cannot justify the position (cf. Nelson and Platnick, 1981) that the only way of discovering a family tree would be to construct the relevant cladogram first. This might be true if all we had was morphology, in a sense, if we were to classify entities with no genetic history, or indeed, assume that the entities had no genetic history. But we do have access to genes of organisms, and their history can be reconstructed, but not through cladistic analysis.

6. Rieppel (1987) confounds his own distinction between pattern and process by allying the contrast to that between hierarchical theories of evolution and Darwinian theories of continuous transformation. Pattern vs. process is equated with hierarchy vs. continuity.

Stratophenetics and the derivative realm

Nelson and Platnick (1981) do not simply have a dichotomy between cladogram and family tree. They describe first-, second- and third-order trees. In a first-order tree all possible ancestors are named, whereas in the second-order all rejectable ancestors are rejected. For the third-order tree no ancestors are named, since in this ideal case we are considering the tree to be an unbroken continuum. In the genetic approach a tree is seen as 'a simple model of the pathways of genetic transmission' (Bishop and Friday, 1985). No ancestors are named and the focus is instead on the unbroken continuity of genetic transmission. For this reason, I descibe the family trees resulting from the genetic approach as third-order, or ideal, trees.

There is an approach to the reconstruction of evolutionary history which attempts to discover possible ancestors. This is the stratophenetic approach (Gingerich, 1979). It assumes that species may be ancestral, and that ancestral species can be discovered through examination of a sufficiently well-preserved fossil record. Cladists have argued that species are to be discovered through cladistic analysis and that they must be considered monophyletic. By definition, then, they cannot be ancestral. Nelson and Platnick (1984) have taken this to mean that the Darwinian theory of

evolution, with its emphasis on ancestral species, is wanting. I argue that species are not discovered through cladistic analysis. They are said to be diagnosed by (aut)apomorphies. However, autapomorphies are not relationships, they are differences. So a species diagnosed by an autapomorphy is in fact diagnosed by a morphological gap, which is not in line with cladistic principles. It is not obvious how a synapomorphy for a species could relate together different life-history stages, different sexes and other morphological variants, such as alternative generations or social castes. A biological (or fundamental) relationship relating these aspects of the species appears to be required first before any cladistic analysis can begin. I suggest that species can only be diagnosed through a consideration of morphological gaps (which is what cladists are doing anyway), together with a consideration of the processes by which biological populations maintain themselves in nature. They exist, in this context, in the derivative realm.

If diagnosed species can be legitimately said to exist in the derivative realm, then there is the possibility that a reconstruction of evolutionary history can also exist there. The fate of morphologically distinct populations can be followed through time with the aid of a well-preserved fossil record. This 'stratophenetic' approach would result in first- and second-order trees, depending on the degree of resolution possible. It is possible that this approach might make use of evolutionary models based on underlying changes in gene frequencies, as described by Felsenstein (1988).

Complementarity applied to natural selection and gradualism

Dynamic and linguistic descriptions are necessary for a complete account of phylogenetic history. This is a logical consequence of Darwin's theory of descent with modification. Descent with modification employs a theory of the organism as both genotype and phenotype, and it is to these two aspects that the dual descriptions apply. Darwin's theory of natural selection can also be described in complementary yet incompatible ways. An account of the stochastic process governing the differential survival of genes from generation to generation provides the dynamic description. An account of the selective benefit of phenotypic traits, and of the patterns of adaptation observable in nature, provides the linguistic description (Allen and Starr, 1982: 57-66). An account of the dynamics of gene transmission acts *a posteriori* as a causal explanation of adaptation: the fit are the ones that have survived. We must remember that the phenotype acts so as to constrain the dynamics of gene transmission. Adaptation is not therefore reducible to

dynamics and in theory may be judged *a priori*, as the selective significance or meaning of the phenotypic feature. The teleological account of adaptation and its mechanistic explanation are equally necessary aspects of the theory of natural selection (Allen and Starr, 1982: 58-59). Description of adaptation is not logically prior to an explanation in terms of genetic dynamics (cf. Brady, 1980). The historical priority in the description of adaptation is because patterns of adaptation, like patterns of organic form, are conspicuous to human observers. As science always begins with observers, it is understandable that investigation of adaptation has generally preceded investigation of its underlying genetic processes.

Complementary aspects of change must be recognised if Darwin's last theory, gradualism, is to be properly understood. Gradual change is to be expected at the genetic level, and at the phenotypic level if there are no significant constraints in the developmental system. The causal explanation of morphological discontinuities, when they occur, is still change in the genotype. We need only propose that the constraints inherent in the developmental system enable a transformation of quantity into quality, from quantitative genetic change to qualitative morphological change.

3.3.6: Summary

In the simple view, a hierarchy consists of a number of structural levels, such as nuclei, atoms, molecules, for which different levels of description are applied for a complete account of the phenomena. In a more sophisticated view, levels in a hierarchy are defined by the descriptions themselves. Each level of a hierarchy requires an alternative description to that which applies to the lower level. Properties emerge at higher levels which cannot be reduced to the behaviour of lower levels. The rules of behaviour of the higher level constrain the dynamics of the lower level. A full account of the hierarchical system is provided by descriptions of both constraints and dynamics. However, it is impossible to reduce one to the other, so the two descriptions are incompatible yet complementary. Descriptions of the organism as genotype and phenotype are alternative, complementary descriptions of the type expected for hierarchical systems. Complex entities are organised as a hierarchy of stable subassemblies. Indeed, it is only hierarchically organised forms which are able to evolve conspicuous complexity. Organisms and lineages of organisms are able to maintain a stability in the face of environmental perturbations. They consist of stable subassemblies, namely homologous organs. In hierarchy theory, a system is seen as a hierarchy of constraints, each acting on the level below in such a way as either to restrict or amplify the information flowing through the system. The phenotype of an organism is to be regarded as a

hierarchy of constraints. These constraints, depending on one's point of view, may be seen as developmental or adaptational and they act so as to maintain the organism as a set of stable subassemblies.

From a hierarchical perspective, cladistic theory is firmly rooted in developmental and evolutionary biology. It is here argued that:

1. The biological basis of homology is developmental constraint. Homologies are relationships of constraint inherited by parts of organisms.
2. A character's coding expresses a set of assumptions about the process by which it has evolved. The ordering and weights associated with states of a character can never be independent of an evolutionary model.
3. Cladogram and tree express different kinds of evolutionary relationships. A cladogram is a hierarchy of types, where a type is the totality of constraints (homologies) inherited by a species. Types are not groups of species, but rather relationships of species. A family tree consists of monophyletic groups of ancestral and descendant species.

The realisation that hierarchy theory is the formal basis of evolutionary theory leads to a renewed emphasis on the morphological aspects of Darwin's theories of evolution:

1. Descent with modification. The material continuity between organisms that Darwin envisaged occurs only in respect of their genotypes. Conventional phylogenetic reconstruction of family trees aims at this genetic aspect. However, organisms are both genotype and phenotype. The history of changes in genetic constitution, on the one hand, and developmental constraints, on the other, may be investigated independently.
2. Natural selection may also be described in terms of genetic dynamics and aspects of constraint. The typical neo-Darwinian, or at least Fisherian, emphasis is on the genetic aspect, neglecting details of the purposive aspect, namely adaptational constraint. A treatment of both mechanistic and teleonomic aspects is necessary for a full account of natural selection.
3. Gradualism. Genetic change may be gradual and continuous, but the properties of the developmental system are such that the phenotypic products of change may emerge discontinuously. The origin of discontinuities in nature need not be ascribed to speciation, but simply the properties of developmental systems.

Complementarity exists at the heart of biology: in the dichotomy between genotype and phenotype, cladogram and tree, and continuity and discontinuity. The striking prediction made in the introduction has been fulfilled. Hierarchy theory is the formal basis of evolutionary theory.

Chapter 4: Scenarios and Relationships of Gadiform Fishes I
A WOGADS Synthesis

Chapter 4.1: Introduction

The most up-to-date collection contributing to an understanding of the relationships of cod-like fishes is *Papers on the Systematics of Gadiform Fishes* (ed. Cohen, 1989). This volume grew out of a Workshop on Gadiform Systematics (WOGADS) held at the Museum of Natural History, Los Angeles County in January 1986. The WOGADS volume represents the intersection of various traditions of investigation, including but not centred on gadiform systematics. The contribution by Patterson and Rosen expresses the culmination of thirty years of work (Rosen, 1962; Rosen and Patterson, 1969; Rosen, 1985). Three papers by Nolf and Steurbaut summarise the conclusions of their examination of otoliths. Markle, Fahay and Dunn have come to a mature appreciation of the power of evidence from developmental osteology to resolve systematic questions (Markle, 1982; Dunn, 1983; Fahay and Markle, 1984; Dunn and Matarese, 1984; see also Markle and Olney, 1990). A cautionary note on the value of developmental stages is provided by Merrett. Howes provides an insight into a novel research programme which continued after the workshop, the combination of osteological and more traditional types of evidence with data on muscles and ligaments (Howes, 1988, 1990, 1991a, 1992, 1993). It was Howes' broader vision that enabled him, from the vantage point of his historical analysis, to probe the interesting biological questions of functional and ecological strategies among gadiforms (Howes, 1988) and biogeography and vertical distribution among gadoids (Howes, 1991b). Fahay and Okamura attempted to resolve the relationships of the enigmatic species *Steindachneria argentea*, and its relationship to macrourids or merlucciids, through a review of osteological characters. A number of other authors turn their specialist expertise to areas of more limited scope (Iwamoto, Fedotov and Bannikov, Inada, Renaud, Paulin).

Howes, Markle and Dunn provide radically new accounts of the history of cod-like fishes, based on their appreciation of cladistic analysis. Nolf and Steurbaut, Okamura, Inada, Iwamoto, Fedotov and Bannikov continue the tradition of the great men of gadiform systematics, Marshall and Cohen (Marshall, 1965, 1966, Marshall and Cohen, 1973, Marshall and Iwamoto, 1973, Cohen, 1984). The Merlucciidae is regarded to involve in or near its scope not only *Merluccius* itself, but also *Macruronus*, *Lyconus* and *Steindachneria*. Marshall's concept of the Merlucciidae is explicitly challenged by Howes and Markle (see especially, Howes, 1991a). The Trachyrincidae,

Bathygadidae and Euclichthyidae traditionally belong to the Macrouroidei, but Howes rejects this arrangement, placing the families within an extended Gadoidei.

Testimony to the fact that we must view the WOGADS volume within the context of its continuing and evolving traditions, Howes has more recently decided against the removal of the Trachyrincidae from the Macrouroidei. The manuscript describing this change was unfortunately never published but a reference to its conclusion is found in Howes (1991b: 595, figure 1). The Macrouroidei consists of the Macrouridae itself, the Trachyrincidae and the Macrouroididae (misprinted as Macrouronidae in the text of Howes, 1991b, and omitted from his figure 1).

Given the diversity of traditions present at WOGADS, how is it possible to provide a synthesis, or come to a consensus? The approach of Nelson (1979) would suggest that the way to discover the pattern of nature beneath different data sets and different methodological approaches is to compare the implied hierarchical classifications. Such consensus techniques have become rather fashionable recently, but have not received unqualified approval. Kluge (1989) has pointed to the difference between summarising most parsimonious solutions for a given data set and summarising the results of analysing different data sets for the same species. Different data sets should be combined in his view, to create a 'total evidence' approach. Such an approach will not blend together hypotheses of relationship with different degrees of support. Instead, dominant hypotheses, well-supported overall, will emerge. If only one contributor has discovered substantial support for a novel arrangement, this will be submerged in any consensus of classifications, but will remain if all evidence is combined. If we wish to understand the functional and biogeographical scenarios associated with the history of the Gadiformes, then a consensus diagram will give a rather nebulous picture.

A partial WOGADS synthesis has already been carried out by Siebert (1990) in the guise of a review of the workshop volume. He analyses characters taken from the cladograms presented by Markle, Nolf and Steurbaut and Howes. My own synthesis grew out of the perception of a number of errors and inconsistencies in Siebert's treatment. The reviewer laments that 'being able to include bathygadids and trachyrincids in the list [of taxa] might have proved interesting' (Siebert, 1990: 890). However, he fails to notice that Markle, in his summary of material examined (p. 60), lists for Macrouridae *sensu lato* only a specimen of *Gadomus arcuatus*, a bathygadid. So the states scored for Siebert's macrourid taxon actually describe a hybrid of bathygadid and macrourid states. Given the importance of Howes' observations of significant differences in the muscles and ligaments of macrourids and bathygadids, this is unfortunate. The Phycidae consists of two parts,

which may not be sister taxa, namely Gaidropsaridae, the rocklings, and the Phycidae *sensu stricto*, the forked hakes. In Nolf and Steurbaut's scheme the Gaidropsaridae and the Ranicipitidae are include within the Lotinae. Siebert also fails to recognise that the traditional arrangement of Nolf and Steurbaut has the Macruronidae included within the Merlucciidae. There are a number of occasions where my interpretation of the author's text differs from Siebert's.

There are five ways in which I have enlarged on Siebert's synthesis. Firstly, I have not restricted myself to the data summarised in cladograms, but also included those presented primarily as lists of characters (Okamura, Iwamoto, Inada). Secondly, I have allowed the characters I am using to be informed by contributions in which information is not presented in either of these formats (Fahay, Merrett, Paulin). Thirdly, I have respected the fact that the authors' contributions belong to a tradition. I have therefore included further information, or qualifications concerning the characters, from a number of earlier sources (Svetovidov, 1948; Rosen, 1962; Rosen and Patterson, 1969; Marshall and Cohen, 1973; Cohen, 1984; Fahay and Markle, 1984; Dunn and Matarese, 1984). The two early papers of Howes (1988, 1989) are essentially a unity and characters and original observations from the former illuminate the content and conclusions of the latter. The characters derived from Howes (1990, 1991a, 1993) are added to strengthen the test of the traditionally accepted hypotheses of relationship. Fourthly, I have included data on the placement of the Gadiformes within the Paracanthopterygii (Patterson and Rosen, Markle P series). I found that many of the relevant characters were also discussed in the context of the relationships of families within the order. In order to assess the polarity of the character states found in gadiforms, I have had to include data on representative taxa from each of the non-gadiform orders. These data have come mainly from the literature, but also through personal observation. Fifthly, I have placed the WOGADS synthesis within the context of acanthomorph relationships as described by Johnson and Patterson (1993). Again it is surprising how many characters relevant to gadiforms are under debate with regard to acanthomorphs as a whole. I have excluded all uninformative characters and those that are not known for all terminal taxa, such as molecular or life history characters. I have confined myself to Recent fishes, ignoring Fedotov and Bannikov's account of fossil gadiforms.

Cohen and Nielsen (1978) divide the ophidiiforms into two suborders according to the mode of reproduction, the oviparous Ophidioidei (Carapidae plus Ophidiidae) and viviparous Bythitoidei (Aphyonidae plus Bythitidae). The Ophidiidae is comprised of four subfamilies, Brotulinae, Brotulataeniinae, Ophidiidae and Neobythitinae and the Bythitidae is comprised of two, Bythitinae and Brosmophycinae. Claims have been made that the Ophidiiformes is non-monophyletic. Patterson and Rosen (1989) regard the ophidioids as paraphyletic and place bythitoids as the sister

group to pediculates plus gadiforms and Markle and Olney (1990) suggest that carapids may be more closely related to lophiiforms. Howes (1992) makes substantial changes to the classification of ophidiiform fishes, particularly with regard to the neobythitine ophidiids. The majority of neobythitines cannot be distinguished from the bythitoids in Howes' scheme (pp. 129-130; table 1; figure 34). Three genera, *Hoplobrotula*, *Sirembo* and *Dicrolene*, remain within the Ophidiidae, specifically as the sister group to the brotulines. Three other neobythitine genera, *Monomitopus*, *Lamprogrammus* and *Glyptophidium*, join the brosmophycine bythitids, *Brosmophyciops* and *Ogilbia*, as the sister group to the other bythitoids (including most neobythitines). They share one synapomorphy with bythitoids, supraorbital trunk of trigeminal nerve complex dividing externally to facialis chamber, but lack the bythitoid condition of reduction or loss of anterior ribs. The five genera show the ophidioid condition, also considered derived, namely a ligamentous connection between the swimbladder and the vertebral column. In addition, *Monomitopus* has the derived form of the interarcual cartilage, large and obliterating the interarcual ligament, found in ophidioids (Patterson and Rosen, 1989: figure 13G). A third brosmophycine genus, *Lucifuga*, also has an intermediate position between the ophidioids and bythitoids. Howes' placement of the extended Brosmophycinae as the sister group to the bythitoids is influenced by Markle and Olney's removal of the carapids from the ophidiiforms. As carapids and ophidiids appear to share good derived characters with the brosmophycines, it is at least as parsimonious that they be considered the sister group to the ophidioids. This question can only be resolved through an analysis of all ophidiiform genera, at least those studied by Howes. Such a project is beyond the scope of this study, which focuses on gadiforms. I therefore follow Howes' modifications, but ignore the brosmophycines, and recognise three terminal taxa of ophidiiforms, namely Carapidae, a reduced Ophidiidae and an extended Bythitoidei.

The full data matrix is shown in Table 2. In the list of characters I use the following abbreviations to describe the different contributions:

jp - Johnson and Patterson (1993: 599-616, figure 24)

pr - Patterson and Rosen (figure 16)

P - Markle (paracanthopterygians: pp. 63-82)

G - Markle (gadiforms: pp. 65-82, figure 19)

ns - Nolf and Steurbaut (1989c: figure 13)

nsa - Nolf and Steurbaut (1989c: figure 13, boxed characters)

h - Howes (figure 10)

ha - Howes (figure 11)

hmacn - Howes (1991a: figure 35)

hmela - Howes (1993: figure 18)

ok - Okamura (pp. 131-138)

iwa - Iwamoto (pp. 163-170)

in - Inada (pp. 199-205, table 1)

d* - Dunn (table 5, all characters)

d - Dunn (table 7, 'decisive' characters)

Inada does not number his characters. The numbering I introduce basically follows the order of the characters as they are listed in the text, except for the upper and lower windows in the suspensorium, which are treated as separate characters as in Inada's table 1. Dunn has two lists, table 5 of all those examined, and table 7 of those characters deemed decisive through an outgroup analysis. Details are not given for all the characters, which is unfortunate, because it is these that are used to discover the relationships of the family Gadidae *sensu stricto* to other families. Even those authors agree that *Merluccius* is placed towards the apex of the Gadoidei far from the basal Macruronidae, disagree as to its sister group, either Gadidae (Howes, Dunn) or Gadidae plus Lotidae (Markle). It is ironic that Siebert (1990: 892) says that Dunn should be commended for the presentation of his characters, in such a way that they facilitate re-examination. For his decisive characters, though, Dunn does provide a clearly set out data matrix. Dunn's conclusions concerning the relationships of gadid genera are contradicted by those of Renaud. However, the latter author does not provide any details of the characters he used in his phenetic analysis.

Chapter 4.2: Data matrix

(1) ha6/ok24/iwa1/iwa2 - size of n (unordered)

0 - small; 1 - large; 2 - absent

The nasals are absent in ophidiiforms (Cohen, 1974: figure 1; Markle and Olney, 1990: figures 21-23; Howes, 1992: figure 2A) and pediculates (Campos, 1972: figure 1; Pietsch, 1981: figures 4, 15-19; Pietsch, 1984: 320).

(2) d*3 (Howes, 1990: 79) - f

0 - not fused; 1 - fused

(3) ok18i/in1/d*10 - V/Y shaped crest

0 - absent; 1 - present

The absence of a V-shaped frontal crest in *Steindachneria* is confirmed by Fahay (1989: 153) and Inada (1989: 199, table 1). Okamura (1989: 133) describes the condition in *Steindachneria* as a modified Y-shaped crest. Observations on rocklings and forked hakes are from Svetovidov (1948). Frontal crests are found batrachoidids (Campos, 1972: figure 1a). Johnson and Patterson (1993: 567-570) describe various patterns of frontal crests in beryciforms and stephanoberyciforms.

(4) ok18ii - relationships of crest

0 - continuous with so; 1 - continuous with par/epo

The frontal crest is continuous with the supraoccipital in batrachoidids (Campos, 1972: figure 1a).

(5) ok19 - posterior connection between f and ps

0 - absent; 1 - present

Okamura (1989: 135) describes a posterior connection between the frontal and the ascending process of the parasphenoid in Moridae (also Okamura, 1970b: 156), Steindachneriidae and Lotidae. Howes (1990: 79) reports a variety of conditions in morids, including that in *Lepidion eques* where ventral laminae are absent. Howes describes the ventral laminae of the Steindachneriidae as 'shallow and widely separated', certainly not in contact with the parasphenoid. Frontal and parasphenoid meet posteriorly in all ophidiiforms according to Okamura (1970b: table 16), but the character appears to be patchily distributed. Contact is present in carapids (Markle and Olney, 1990: figures 21 and 22), in the ophidiids *Brotula*, *Hoplobrotula*, *Otophidium* and *Sirembo* (Okamura, 1970b: 153) and *Enchelybrotula* (Cohen, 1982: figure 1) and in the bythitoid *Neobythites* (Okamura, 1970b: 153); but absent in the ophidiid *Brotulataenia* (Cohen, 1974: figure 1) and the bythitoid *Acanthonus* (Howes, 1992: figure 8).

(6) ok16/ok17/iwa3/in3 - relationship between me and ps

0 - ps bar-like, not fused to me; 1 - ps has vertical plate; me extends posteriorly and is constricted by vertical plate of ps

Okamura (1989: 133) has the shape and connections of the parasphenoid as separate characters, but it is clear that they are logically dependent. Howes (1990: 81) points out that in *Muraenolepis* it is a median lamina, not a pair of lateral laminae, that contact the mesethmoid.

(7) ok14 - ethc

0 - extends posteriad along ps; 1 - forms vertical plate behind me

The ethmovomer of *Melanonus*, *Opsanus*, *Lophius*, *Aphredoderus* and *Percopsis* are illustrated by Stiassny (1986: figures 21d, 21e, 21f, 21g, 22f, 22g) in which the ethmoid cartilage extends along the parasphenoid. However, in *Carapus* (Stiassny, 1986: figure 21d) and the bythitoid *Acanthonus* (Howes, 1992: figures 2A, 2B) the ethmoid cartilage is high and does not extend along the parasphenoid. Similarly, in the ophidiid *Brotulataenia* the mesethmoid forms a 'hood' over the high ethmoid cartilage (Cohen, 1974: 121).

(8) hmacn14 - cone-shaped le wing

0 - absent; 1 - present

The distribution is given according to the discussion in Howes (1991a: 104), not according to the paper's synapomorphy scheme (Howes, 1991a: figure 35).

(9) hmacn10 - firm articulation between io1 and le wing

0 - absent; 1 - present

This character is inapplicable to lophiiforms because the infraorbital series is lacking.

(10) hmacn6/hmela14 - pal contacts ethmovomerine bloc

0 - no; 1 - yes

(11) h10/hmacn9 - le-pal ligament

0 - present; 1 - absent

The Bregmacerotidae is excluded from a clade defined by the absence of the lateral ethmoid-palatine ligament in Howes (1989: figure 10), but included in such a clade in Howes (1991a: figure 35). Absence of the ligament is confirmed in Howes (1991a: 104).

(12) ok15 - contact between le and ps

0 - absent, le supported ventrally by ethc; 1 - narrow; 2 - broad; 3 - very broad

The concept of this character provided by Okamura (1989: 133) is of simple presence versus absence of contact between the lateral ethmoid and parasphenoid. Detail on the degree of contact is provided by Howes (1990: 82).

(13) ok13/in4 - teeth on vo

0 - present; 1 - absent

Svetovidov (1948) reports that teeth are usually present, but occasionally absent in morids. Vomerine teeth are absent in percopsids (Rosen and Patterson, 1969: table 1).

(14) Howes (1990: 80-81) - spo (unordered)

0 - visible dorsally but not enlarged; 1 - reduced, not visible dorsally; 2 - enlarged, flaring laterally

The sphenotic is prominently flared in pediculates (Lauder and Liem, 1983: figure 37, character 17).

(15) hmacnh3/ok20 - deep fossa within pts/spo/pro anteriorly accommodating io6

0 - absent; 1 - present

This character is inapplicable to pediculates which lack the sixth infraorbital.

(16) pr8 - posterior myodome

0 - present; 1 - absent

(17) ha1/hmacn2/hmela1/ok20/in2 - foramina for cranial nerves in pro

0 - present; 1 - absent

The gadiform condition is that foramina are absent from the prootic (Gosline, 1968; Patterson and Rosen, 1989: 17-18, 29). (Contradictory observations are made by Okamura, 1989: 135, and Inada, 1989: 199-200, Table 1.) Foramina are absent from the prootic in the bythitoids *Acanthonus*, *Bassozetus*, and *Abyssobrotula* (Howes, 1992: 104).

(18) Howes (1990: 82) - direction of notches for optic and trigeminal nerves (unordered)

0 - anterior part of pro medially directed so that border of optic foramen orientated transversely; 1 - trigeminal notch in sagittal plane, pro wall thickened posterior to notch; 2 - thin walled pro with deeply indented notch for optic and trigeminal nerves

This character is inapplicable to non-gadiform paracanthopterygians since the nerves pass through the prootic rather than notching it.

(19) hmacn16 - horizontal shelf extending from side wall of pro

0 - absent; 1 - present

The description of this character comes from (Howes, 1991a: 98).

(20) Howes (1991a: 98) pro with transverse septum

0 - absent; 1 - present

(21) pr14iv - ic

0 - present; 1 - absent

(22) Howes (1990: 82, 89) - so crest

0 - present; 1 - reduced; 2 - absent

(23) hmela6 - border of foramen magnum

0 - so included; 1 - so excluded

Howes (1992: 128) reports that the supraoccipital is excluded from the border of the foramen magnum in ophidiiforms. The derived state also occurs in some macrourids (Okamura, 1970b: figures 34H, 34I; pers. obs.).

ok8 - enlarged scales in exo sensory canal

Okamura (1970b: figure 9) illustrates five so-called modified or enlarged scales in the occipital canal of *Caelorinchus multispinulosus*, one positioned over the parietal, three placed more ventrally over the pterotic and one hinged to the back of the skull which transfers the occipital sensory canal to a lateral line scale. Comparing Okamura's figure to those of *Notropis bifrenatus*, a cyprinid (Harrington, 1955: figures 1, 4), suggests that these structures are not scales at all. The parietal has a canal-bearing counterpart, the medial extrascapular or "postparietal". A membranous bone overlying the pterotic is described as a supratemporal and has an associated canal bone, the lateral extrascapular. The posttemporal is a superficial bone with a canal component, which is hinged to the back of the skull and transfers the sensory canal via to the supracleithrum to the lateral line scales. Okamura's dorsalmost scale bone appears to be the medial extrascapular, the three covering the pterotic the supratemporal and/or lateral extrascapulars. Jollie (1986: 368) describes the supratemporal as an intertemporo-supratemporotabular, evidence for fusion being that three canal bones appear during development. It is curious that this is the same as the number of Okamura's scale bones which overly the pterotic. It is also strange that a bone which appears to take the same position as the posttemporal in *Notropis* is present in macrourids at the same time as the typical forked, deeper-lying posttemporal. Unfortunately, the distinction between states that Okamura (1989: 132) proposes is vague, either not 'strongly expressed' or 'notable', and I have not included the character in the analysis.

(24) pr14ii - posttemporal fused to skull

0 - no; 1 - yes

(25) ok9/d6 - number of io bones

0 - six; 1 - five; 2 - one; 3 - none

Dunn (1989: 217) assumes that gadids have gained an extra infraorbital, that the Merlucciidae, with five infraorbitals, possess the primitive state. Six, however, is the primitive number for gadiforms, and is found in percopsiform and ophidiiform outgroups. The infraorbital series is reduced in pediculates. Only the lachrymal remains in batrachoidids and the series is completely absent in lophiiforms (Gill, in press).

(26) Rosen (1985: 43) - pm

0 - unsegmented; 1 - segmented

(27) pr7 - "gadoid notch" i.e. excavation behind postmaxillary process of pm

0 - absent; 1 - present

The character is inapplicable to aphredoderoids, because the premaxilla is segmented. Howes (1993: 19) states that in *Melanonus* there is no gadoid notch at the base of the postmaxillary process.

(28) pr14v - partially or completely independent ascending process of pm

0 - no; 1 - yes

h18 - attachment of m-pm ligament

Howes (1988: 6-7) describes a condition of the attachment of the anterior maxillo-premaxillary ligament that is unque to macrouroids (Macrouridae plus Macrouroididae), namely via the rostral cartilage to a thick cartilaginous meniscus covering the maxillary head (Howes, 1988: figures 28B, 28C). However, Howes (1989: figure 10) regards this same condition as an autapomorphy of the Macrouridae. In the Trachyrincidae and Bathygadidae, the attachment is said to via a 'cylindrical chondroid or fibrous element whose posterior tip joins a thin ligament stretching caudally, which becomes incorporated with the connective tissue stretching between the maxilla and premaxilla' (Howes, 1988: 7). This complex association between the ligament and other connective tissues, suggests that the ligament may appear in response to mechanical needs which will vary even within the same group. In other families, Howes states that the ligament attaches directly to head of the maxilla or via a thin meniscus, but in practice it is difficult to establish the presence or absence of a thin meniscus, especially in small specimens. Howes also notes that the ligament is lacking in certain taxa, for example *Euclichthys*, and I was unable to find it in *Bregmaceros* and the morid *Lepidion eques*, which again questions the homology of the ligament in those taxa where it appears.

(29) hmela10 - pal forming hinge or butt joint with ent and ect

0 - absent; 1 - present

Rosen and Patterson (1969: table 1) and Howes (1993: 20) record the derived state in percopsids.

(30) pr14i - ent

0 - present; 1 - absent

Howes (1990: 85) states that there is only one pterygoid element in *Bregmaceros*, which, judging by its position, is most likely the ectopterygoid.

(31) Howes (1990: 85) - ent confined above anterior half of ect

0 - no; 1 - yes

(32) Howes (1990: 85-86) - reduction in size of ect

0 - no reduction; 1 - general reduction; 2 - further reduction

(33) Howes (1990: 86) - wide separation of qp from qb

0 - absent; 1 - present

(34) Howes (1990: 85) - sym

0 - narrow stem, broad head; 1 - triangular to oblong, no stem

(35) Howes (1990: 86) - sym process of pop (unordered)

0 - contacts sym head and ventral border of hyo; 1 - contacts sym cartilage; 2 - contacts lateral face of hyo

(36) ok11/in6 - hyo-pop (upper) window

0 - absent; 1 - present

Upper and lower windows are variably present in lophiiforms (Pietsch, 1981: figure 9, 21-25).

(37) ok12/in7 - sym-pop (lower) window

0 - absent; 1 - small; 2 - large

Further detail on the size of the lower window is provided by Howes (1990: 85).

(38) hmacn13i/d14- pop process of hyo

0 - absent; 1 - present

The standard terminology for the structure that Howes (1991a) calls the lateral flange is that of Svetovidov (1948: Figure 10), namely the preopercular process. In Howes (1990: 84-85), written after Howes (1991a), this terminology is adopted. The character describing the orientation of the process is taken from Howes (1990) and the distribution given is modified according to the observations given in Dunn (1989: 224).

(39) hmacn13ii/d14 - orientation of pop process of hyo

0 - horizontal; 1 - ventral

(40) ha3/hmela4 - foramen for mandibular branch of hyomandibular facial nerve in anterior strut of hyomandibula

0 - present; 1 - absent

A foramen for the mandibular branch pierces the anterior strut of the hyomandibula in all non-gadiform paracanthopterygians, except *Acanthonus* (Howes, 1992: 103). Howes (1993: figure 18) describes attrition of lateral face of hyomandibula as a synapomorphy of all gadiforms, following Gosline (1968). However, this conflicts with his earlier discussions of the character. According to Howes (1989: figure 11) the hyomandibula of Melanonidae, Steindachneriidae, Bathygadidae, Moridae, Trachyrincidae, Macrouroididae and Macrouridae is reduced, the mandibular branch of the hyomandibular facial nerve passing anterior to it. The primitive state is for the mandibular branch to pass through a foramen in the anterior strut of the hyomandibula. No observations are reported explicitly by Howes (1989: 124) for the primitive state in Euclichthyidae, Bregmacerotidae and Merlucciidae, or for the derived state in Moridae or Macruronidae. The nerve pathway pierces the hyomandibula in *Euclichthys* (Howes, 1988: figure 15). Howes (1989: figures 9A, 9B) records the state in *Gadomus* as derived, the state in *Bathygadus* as primitive. Howes (1990: figure 13) shows that *Macruronus* possesses the primitive state. The foramen is present in Moridae, Bregmacerotidae and Merlucciidae (pers. obs.).

(41) h1/h9/hmacn7 - plane of A

0 - entire A1b medial with respect to other elements; 1 - anterior part of A1b medial with respect to other elements; 2 - elements lie in same plane

Howes (1989: 118) states that the widespread condition in acanthomorphs is for A1b to lie medial to A1a. However, in Howes (1989: figure 10) adductor muscles lying in the same plane is taken as primitive for gadiforms, with progressive reversals to the medial state appearing as separate synapomorphies [h9a, h9b=hmacn7]. He also ignores an earlier statement that the

Bregmacerotidae 'do not have the gadoid arrangement of adductor muscles' (Howes, 1988: 34; see following character).

(42) h5 - A1

0 - divided; 1 - incompletely divided; 2 - single

In general, paracanthopterygians have two segments of the first adductor, namely A1a, an outer, more ventral segment which may be more or less closely associated with A2; and A1b, an inner, more dorsal element (Winterbottom, 1974: 231). Both segments primitively originate from the hyomandibula (Winterbottom, 1974: 231, 233; Howes, 1992: 122-123; Field, 1966: 3A; Pietsch and Grobecker, 1987: figure 151). In all ophidiiforms, except *Acanthonus*, A1b is divided by the *levator arcus palatini* into lateral and medial components, the medial originating from the pterygoids and the lateral from the hyomandibula (Howes, 1992: 122-123). In many gadiforms, there is partial or complete fusion between A1a and A1b elements. I interpret the two ligamentous connections from the single A1 element in *Trachyrincus* as homologous to the connections of the A1a and A1b muscles respectively (see Howes, 1988: 34). The single A1 in the Macrouroididae is then homologous to that in Trachyrincidae, despite having lost one of the ligaments (Howes, 1988: 15). *Bregmaceros* and *Muraenolepis* have a single A1 element (Howes, 1988: figures 22A, 22B; 1991a: figure 35, hmacni). Howes (1988: 34) reports incomplete subdivision of A1 in *Euclichthys*, *Steindachneria*, a single morid genus *Lepidion*, and *Lyconus*. In some Macrouridae the first adductor is incompletely divided, namely *Hymenocephalus*, *Echinomacrurus*, *Sphagemacrurus*, *Cetonurus*, *Mataeocephalus*, *Macrosmia*, *Ventrifossa*, *Malacocephalus*, *Odontomacrurus* and *Cynomacrurus*, whereas in other genera A1 is completely divided (Howes, 1988: table 1).

(43) Howes (1992: 122-123) A1b

0 - not divided into lateral and medial components; 1 - divided into lateral and medial components

(44) h7 - constriction and preorbital expansion of A1/A1b

0 - absent; 1 - tendinous constriction; 2 - present

(45) h11 - origination of A1b (unordered)

0 - from hyo; 1 - from pop limb; 2 - from fascia of A2; 3 - from fascia of lap; 4 - partly anteriorly from pal

Extra data for this character are taken from the descriptions of each family and the discussion of other paracanthopterygians provided by Howes (1988). Howes (1991a: 98) confirms that A1b

originates from the palatine in *Merluccius*, *Macruronus* and *Lyconus* (cf. Howes, 1991a: figure 35, hmacnh, hmacnp).

(46) h12 - site of attachment of muscle A1/A1b to m

0 - laterally, ventral limb of head; 1 - medial aspect of head; 2 - dorsomedial ledge; 3 - ventromedial process

This character is inapplicable to macrouroidids since A1 attaches to the maxilla via the maxillo-mandibular ligament.

(47) h1/hmacn1/hmela5 - position of lap with respect to A complex

0 - medial to A complex; 1 - mostly medial, partially lateral to A complex; 2 - lateral to adductor complex

Howes (1989: figure 10) has *levator arcus palatini* lateral to adductor complex as a synapomorphy of gadiforms. However, he notes (p. 118) that in *Trachyrincus*, the Gadidae, Lotidae, Gaidropsaridae, Phycidae and Muraenolepididae, the muscle occupies a medial position, the common state in other acanthomorphs. *Euclichthys* has an intermediate condition.

(48) Howes (1988: 39-40) - aap

0 - undivided; 1 - divided

(49) Howes (1988: 39-40) - aap insertion

0 - posterior; 1 - anterior, as far as pal

An anterior insertion for the *adductor arcus palatini* is found in all gadiforms, except morids (Howes, 1988: 20), bathygadids and euclichthyids (Howes, 1988: 40).

(50) h3 - ligamentous coupling between op series and lower jaw

0 - op-sop-iop; 1 - op/sop/pop/hyo-iop

In acanthomorphs, lowering of the lower jaw is primitively accomplished by the *levator operculi* acting through the opercular bones by a series of ligamentous connections: operculum to suboperculum to interoperculum to lower jaw (Howes, 1989: 116). However, the primitive state for gadiforms, present in all except the Macrouridae and Macrouroididae, the preoperculum and hyomandibula are involved in this series (Howes, 1988: 9-10; Howes, 1989: 116-117). There is an error in Howes (1991a: figure 35, hmacna) where the Macrouridae and Macrouroididae are said to have lost the ligamentous connection between the suboperculum and interoperculum. Howes and

Crimmen (1990: 184) record a ligamentous connection between the interoperculum and hyomandibula in bythitoid ophidiiforms.

(51) h15 - epaxial muscle segment inserting on inner face of op

0 - absent; 1 - present

Howes (1990: 89-90) rejects his earlier interpretation of the condition in *Muraenolepis*: 'the so-called *epaxialis* could well be a *levator operculi* of shifted origin.' In Howes (1991a: figure 35, hmacnl) this character is given as a possible synapomorphy of the Phycidae.

(52) P11 - complex strut joint between ach and hhs

0 - absent; 1 - present

(53) P10/G16/ha2/hmacn11 - connection between pch and iop

0 - ligamentous connection; 1 - joint

Markle (1989: 70) considers that a joint between the posterior ceratohyal and the interoperculum is primitively present in gadiforms, since it is present in batrachoidiforms and gobiesociforms. It is, however, absent from most lophiiforms and from ophidiiforms. A specimen of *Lyconus* examined by Markle specifically for this character was found to lack the joint. The joint is also absent in Melanonidae, Moridae, Euclichthyidae and Steindachneriidae. Howes (1989: figure 10) reports the joint to be present in Trachyrincidae, and absent in Macrouridae and Macrouroididae, however the joint is present in *Macrouroides* (pers. obs.). Howes (1990: 89) includes the Macruronidae in a group defined by the presence of the joint, although later (Howes, 1991a: figure 35) he excludes it, along with *Bregmaceros* and *Euclichthys*, from such a group. Howes (1991a: table 1, see figure 16) reports that the joint is absent in the Macruronidae, and (p. 104) states that 'an interopercular-interhyal [posterior ceratohyal?] joint' is absent in *Bregmaceros* and only a shallow interopercular fossa is present in *Euclichthys*.

(54) ok10/iwa7 - number of br rays (unordered)

0 - seven; 1 - six; 2 - eight

Six branchiostegal rays are found in some macrourids, but seven is the primitive number for gadiforms. Six branchiostegals are found in percopsiforms and pediculates, seven in carapids and ophidiids, eight in bythitoids, though there is some variation in individual groups (McAllister, 1968).

(55) G17/ok10/iwa6 - position of uppermost four br rays (unordered)

0 - 2½-3 rays on ach, 1-1½ on pch; 1 - 2 rays on ach, 2 on pch; 2 - 4 rays on ach, 0 on pch

Since the number of branchiostegal rays is variable in paracanthopterygians, only the uppermost four are counted here. These four are distinguished by their cup-shaped articulations with the hyoid bar. Branchiostegal rays inserting on cartilaginous matrix between the anterior and posterior ceratohyals are counted as half on each (see McAllister, 1968). Percopsiforms exhibit state 0; ophidiiforms and batrachoidids state 1; lophiiforms have either state 0 or state 2 (McAllister, 1968).

(56) jp26/pr10/G4/G7/G9 - IAC

0 - absent; 1 - small, ovoid; 2 - large, rod-like

The interarcual cartilage is absent in percopsiforms, bythitoids and pediculates, so I have taken this to be the primitive state. Patterson and Rosen (1989: 25) favour a hypothesis of parallelism to account for the cartilage's absence in percopsiforms. If an interarcual element is present, then an uncinate process must be present on the first epibranchial. Presence or absence of the uncinate process is therefore only applicable if both elements are absent. Travers (1981: 856-857, 864-867) describes the interarcual cartilage in paracanthopterygians. In *Bathygadus*, a small interarcual cartilage lies well away from the uncinate process of the first epibranchial, within a 'collagenous strand' (the interarcual ligament) which connects the uncinate process to the second pharyngobranchial (cf. *Gadomus arcuatus*, Markle, 1989: figure 3B). A similar condition is found in *Macrouroides* (pers. obs.) where a small cartilage lies distant from the uncinate process. The cartilage is absent in *Trachyrincus* (Travers, 1981: 856). Travers (1981: 864) describes the interarcual cartilage and the uncinate process on the first epibranchial as absent in the bythitoid *Oligopus ater*. However, as his figure shows (figure 11), and as can be seen from the illustration of *Oligopus claudei* in Patterson and Rosen (1989: figure 13J), the uncinate process is still present, but is not cartilage filled. Johnson and Patterson (1993: 613) state that a small, ovoid cartilage is found in anomalopids, melamphaeids and some myctophids, and describe a large, rod-like interarcual cartilage as a synapomorphy of an extended Percomorpha (including the atherinomorphs). The interarcual cartilage is absent, though, in a number of percomorph groups, namely *Elassoma*, all gasterosteiforms except aulostomids, echeneids, blennioids, gobiesocoids and acanthuroids.

(57) G5/8 - IAL

0 - present; 1 - absent

(58) G12/d23 - uncinate process on eb1

0 - present; 1 - absent

(59) P8/G14 - ligamentous connection between eb1 and eb2

0 - present; 1 - absent

(60) pr15/P3/G2 (in part) - pb1

0 - ossified; 1 - cartilaginous or lost

Markle (1989: 65) describes an ossified first pharyngobranchial in *Melanonus*. However, Howes (1993: figure 11B) records a cartilaginous element for that taxon.

(61) P4ii/G6 - articular surface of pb2 (unordered)

0 - strut-like, contacts uncinate process of eb1; 1 - strut-like, contacts distal tip of eb1;

2 - broad, contacts uncinate process of eb1

This character is inapplicable to bregmacerotids because they have lost the second pharyngobranchial (see Markle, 1989: G1/G10). The articular surface contacts the uncinate process in percopsiforms, carapine carapids and ophidiids. The articular surface contacts the distal tip in pyramodontine carapids and most bythitoids. In lophiiforms the first epibranchial falls short of the second pharyngobranchial.

(62) pr12/P5/P6/P7 - pb3

0 - elongate, without multiple articulation with eb2-4; 1 - "bear's paw" shape, short and broad, with three finger-like uncinate processes articulating tips of eb2-4

(63) P9 - contact between pb2/3 and eb2

0 - eb2 contacts pb3; 1 - eb2 contacts only pb2

(64) h2/8i - *obliqui ventrales* on first gill arch

0 - complete; 1 - almost entirely tendinous; 2 - entirely tendinous or absent

Characters h2/8i and h2/8ii express the observations recorded in Howes (1988: 46; 1989: 115-116).

(65) h2/8ii - *obliqui ventrales* on second gill arch

0 - complete; 1 - weak; 2 - entirely tendinous or absent

(66) Howes (1988: 46-48, table 2) - insertion of *rectus ventralis IV* (unordered)

0 - hb3; 1 - uh; 2 - dorsal aponeurosis of sh

(67) h4/h14i - *rectus communis* attachment (unordered)

0 - inserts entirely on uh; 1 - attached partly to uh, partly to sh; 2 - fully attached to sh

I have lumped together and reorganised Howes' characters relating to the attachment of the *sternohyoideus* to the *rectus communis* [h4a, h4b, h14] in order to accommodate observations recorded in Howes (1988: 46-48, table 2; 1989: 116). The Bregmacerotidae and Macrouroididae are omitted from table 2 even though they are discussed in the text. A sternohyoideus attachment is given for the Lotidae, although a urohyal attachment is reported elsewhere (Howes, 1988: 47; 1989: 116). A *sternohyoideus* attachment for the *rectus communis* is the only character state defining the Gadoidei of Howes (1991a: hmacn3; 1993: hmela12), even though it is present in some macrourids, namely *Hymenocephalus*, *Nezumia*, *Ventrifossa*, *Odontomacrurus* and *Cynomacrurus* (Howes, 1988: table 1). In *Melanonus* the *rectus communis* does not attach, directly or indirectly, to the *sternohyoideus* but to the urohyal and third hypobranchial (Howes, 1988: table 2; Howes, 1993: 30). The *rectus communis* attaches to the anterior tip of the urohyal in most ophidiiforms, but the attachment of the muscle is variable in ophidiids (Howes, 1992: 125-126, figure 29B). In the ophidiines, *Ophidion*, *Genypterus* and *Lepophidium*, the *rectus communis* attaches to the lateral face of the urohyal, at its broad, canopy-like base.

(68) h4/14ii - detail of *rectus communis* attachment (unordered)

0 - on lateral face of uh; 1 - on anterior tip of uh; 2 - to dorsal surface of sh; 3 - to an internal myocomma of sh; 4 - via tendinous aponeurosis to sh

(69) Howes (1988: 44-46) sh

0 - stout, broad; 1 - long, compressed

The *sternohyoideus* is long in some ophidiiforms, namely the ophidiids *Hoplobrotula*, *Sirembo* and *Dicrolene* and the bythitoid *Acanthonus* (Howes, 1992: 124).

(70) Howes (1988: 44-46) stout sh associated with uh that is widely separated from pelv girdle

0 - absent; 1 - present

(71) h13/h16/hmacn12 - insertion of *retractor dorsalis* (unordered)

0 - inserts on pb3 and pb4; 1 - inserts on pb3; 2 - inserts on pb4

This character is also discussed in Howes (1988: 48).

(72) ok25/in11 - relation between cranium and first centrum

0 - attached but not fused to exo and bo condyles; 1 - fused to exo and bo condyles

(73) pr13/ok26/in11/d7 - first neural spine

0 - free; 1 - immovably fused to so

The condition of first neural spine joined to the supraoccipital crest is 'universal in pediculates' (Patterson and Rosen, 1989: 27). Howes and Crimmen (1990: 185) report fusion between the first neural arch and the supraoccipital crest in bythitoids. Extra details on gadiform families are provided by Okamura (1970b: 99), Cohen (1984: 261), Patterson and Rosen (1989: 14, 27), Fahay (1989: 150), Howes and Crimmen (1990: 157). Inada (1989: 202-203) describes the condition in Gadidae as free, whereas Dunn (1989: 217) follows Svetovidov (1948) and describes the condition as fused. The supraoccipital crest is lacking in *Bregmaceros* (Markle, 1989: 78-79; Howes, 1990: 82, 89).

(74) ok27i - anteriormost neural spines (unordered)

0 - unmodified; 1 - 1st reduced; 2 - 1st enlarged (2nd and 3rd as well in some)

The first neural spine is always reduced relative to the second in ophidiiforms (Markle and Olney, 1990: 278).

(75) ok27ii - number of anteriormost neural spines enlarged

0 - 1st; 1 - 1st and 2nd; 2 - 1st, 2nd and 3rd

(76) ok28 - enlargement of anteriormost neural spines followed by shortening of subsequent neural spines

0 - no; 1 - yes

(77) pr6/16 - plane of exo condyles

0 - exo condyles posterior to plane of bo condyle; 1 - exo condyles displaced forward from plane of bo condyle, with corresponding extension of "prezygapophyses" on v1

(78) pr11 - exo condyles

0 - planar, forming a continuous articulatory surface with v1; 1 - exo facets "cod-like", condyles widely separated, cartilage-filled and tube-like, articulating with comparably modified "prezygapophyses" on the first centrum

According to Rosen (1985) and Patterson and Rosen (1989: 27) ophidioid ophidiiforms have the primitive planar arrangement of exoccipital condyles, whereas bythitoids show the derived state. However, Howes (1992: 110, figures 16-18) shows that the derived state occurs only in *Acanthonus armatus*.

(79) pr3 - supraneurals ossified

0 - cartilaginous or lost; 1 - ossified, both ends tipped with cartilage; 2 - ossified, both ends enclosed in bone

Patterson (1989: 20-22) give a detailed discussion of the issue of supraneurals and predorsals in paracanthopterygians, and describe the diversity of conditions in ophidiiforms (see also Markle and Olney, 1990: 278). Johnson and Patterson (1993: 609) describe distal ossification of the supraneurals as synapomorphic for beryciforms (excluding stephanoberyciforms) and percomorphs (including atherinomorphs). They note that this derived state also occurs in percopsiforms. In those gadiforms where ossified supraneurals occur, namely *Raniceps*, Phycidae, the gaidropsarid genus *Ciliata* and Euclichthyidae, they are cartilage-tipped. Supraneurals are lost in pediculates, some ophidiiforms and most gadiforms, but also (supposedly secondarily) in some percomorphs, namely *Elassoma*, gasterosteiforms, synbranchiforms and many perciforms, such as gobioids, blennioids and scombroids (Johnson and Patterson, 1993: 560).

(80) pr5 - anterior centra

0 - equal in size; 1 - second centrum, or second and third, foreshortened, much shorter than first and third or fourth

(81) pr9i/ok30/in13 - position of first parapophysis

0 - 3rd or more anteriorly; 1 - 4th; 2 - 5th; 3 - 6th; 4 - 7th

In *Melanonus* the first parapophysis occurs on the fifth vertebra (Howes, 1993: figure 14A) and not on the third as stated by Okamura. The latter condition, unusual for gadiforms, is found in *Bregmaceros* (Howes, 1993: 25, figure 14B; pers. obs.).

pr9ii/ok31/in15 - number of pleural ribs directly attached to centra

As implied in the coding adopted by Patterson and Rosen (1989: figure 16), this character is correlated with pr9i. If the first parapophysis occurs on the fourth or fifth vertebra, then there are two pleural ribs attached directly to centra. If the first parapophysis occurs on the sixth or seventh vertebra, then there are three or four ribs attached directly to centra. Okamura's (1989: 137)

observation of five pleural ribs attaching directly to centra in *Brotula* is mistaken. These are epineurals (see Patterson and Rosen, 1989: figures 8A, 8B; Patterson and Johnson, 1995).

(82) pr14iii/P20 - pleural ribs

0 - present; 1 - absent

Pleural ribs are absent in pediculates, but also in carapine carapids (Markle and Olney, 1990: 281).

(83) ok32 - shape of pleural ribs

0 - long; 1 - short, rod-like

(84) pr18/P18/P19/hmela2 - epineurals on first two vertebrae

0 - present; 1 - absent

Patterson and Johnson (1995:43) describe the single series of intermusculars in paracanthopterygians as epineurals. Epicentral ligaments and epipleurals are absent. The descent of the epineurals into the horizontal septum occurs in holacanthopterygians, that is, acanthomorphs minus Lampridiformes and Polymixiiformes (Johnson and Patterson, 1993: 603, jp14).

ok33/in16 - epineurals

Okamura (1989: 137) and Inada (1989: 205) argue that the presence of numerous epineurals, say from eight to thirty-three, is the primitive state, with between zero and six bones as derived. Patterson and Johnson (1995: 43) argue that the primitive state is a short series of five to eight epineural bones. Applying this to Okamura's data ten or more becomes the derived state. *Urophycis* has seven epineural bones, however, and *Oligopus*, a bythitoid, has nine (pers. obs.). I judge that there is no distinction between states, simply a general trend, which itself is difficult to polarise. Epineural bones are absent in *Bregmaceros* (Markle, 1989: 73).

(85) P23/ok27 - connection between vertebral column and swimbladder

0 - none; 1 - ligamentous connection from two anterior ribs; 2 - direct connection to vertebral centra and parapophyses

Rosen and Patterson (1969) note that many gadiforms and ophidiiforms have a connection between the swimbladder and the vertebral column. Markle (1989: 82) disagrees with their contention of relationship between the two groups on this basis, commenting that the condition in gadiforms is more like that in sciaenids, which have drumming muscles. Marshall and Cohen (1973: 486-487) report drumming muscles in Lotidae, Gadidae, Phycidae and Ranicipitidae. Howes (1992: table 1) summarises divergent specialisations of the swimbladder in ophidiiforms. Ophidiids have a

ligamentous connection between the swimbladder and the anterior ribs, but, in bythitids, the swimbladder is situated posteriorly, unmodified except for muscle attachment. Markle and Olney (1990: 282) state that the ligamentous connection between the swimbladder and the vertebral column is absent in *Brotula*, but this is contradicted by Howes. Okamura (1989: 137) claims that the swimbladder is lost in *Squalogadus* and *Melanonus*, but Howes (1993: 28) confirms its presence in *Melanonus*.

ok35 - pelv girdle

Okamura (1989: 137) distinguishes two conditions of the pelvic girdle, set posteriorly and set anteriorly, between the cleithra or further forward. Macrourids and macrourids are supposed to show the contrast between the two states, posterior and anterior respectively, but I have been unable to make such a distinction through personal observations. The pelvic girdle in *Merluccius merluccius* is close behind the cleithrum, but the lower limb of the cleithrum projects further forward, giving the impression that the pelvic girdle is set well forward. In *Caelorinchus caribbaeus* the lower limb of the cleithrum is straighter and gives the impression that the pelvic girdle is set further back. I believe that the distinction between states is unclear, and complicated by differences in the degree of curvature of the cleithral lower limb.

(86) jp29/iwa18 - reduced pelv

0 - absent; 1 - present

Johnson and Patterson (1993: 613-614) propose reduction of the pelvics to six or fewer rays as a synapomorphy of their Percomorpha (including atherinomorphs). They note that reduced pelvics are also found in ophidiiforms, pediculates, various gadiforms (see Markle, 1982: table 3; Fahay and Markle, 1984: table 72; Houde, 1984: 307; Cohen *et al.*, 1990), all stephanoberyciforms, except melamphaeids and *Hispidoberyx*, many of the elongate lampridiforms, anomalopid and monocentrid beryciforms, and the zeiform *Pseudocyttus*.

(87) P16/17 - origin of Baudelot's ligament

0 - first centrum or more posteriorly; 1 - occiput

Johnson and Patterson (1993: 605-606, jp18) describe an occipital origin for Baudelot's ligament originates as a synapomorphy of zeiforms (excluding caproids) and euacanthopterygians (beryciform, excluding stephanoberyciforms, plus percomorphs, including atherinomorphs). The ligament originates from the exoccipital in zeiforms and from the basioccipital in percomorphs. The ligament originates from the basioccipital in batrachoidiforms and ophidiiforms (Howes, 1992: figure 17A). Johnson and Patterson (1993: 605; Patterson and Johnson, 1995: 42) note several

other instances of homoplasy. In veliferid lampridiforms, a portion of Baudelot's ligament inserts on the exoccipital. Among stephanoberyciforms, *Rondeletia* and cetomimids have two ligaments, one from the first vertebra and one from the basioccipital. The ligament is also double in the xenisthmid gobioid *Tyson.* Among percomorphs, agonid and hexagrammid scorpaeniforms, champsodontids and some zoarcoids have the ligament originating from the first vertebra. In certain euacanthopterygian groups, the ligament is absent, namely the beryciforms *Anoplogaster* and *Monocentris*, dactylopterids, synbranchiforms, gasterosteiforms, gobiesocids and callionymids.

(88) P14 - expanded distal pec radial

0 - absent; 1 - present

Markle (1989: 72) notes an expanded distal pectoral radial is found carapids, aphyonid bythitoids, ceratioid lophiiforms and batrachoidids (see also Markle and Olney, 1990: 286-287). The structure is cartilaginous in carapids and batrachoidids, but ossifies in other groups. Johnson and Brothers (1993: 463-464) describe what appears to be a cartilaginous distal radial in *Schindleria*, which they regard as a gobioid: 'We have been unable to resolve unequivocally the origin of this cartilaginous element, but it appears that rather than being part of the distal radial series it may originate as part of the coracoscapular cartilage. In any case, it soon fuses to the base of the medial half of the first ray, continues to grow laterally and eventually ossifies to form the articular facet that abuts the scapular condyle.' If their interpretation holds for paracanthopterygians, then the contrast is not between whether the distal radial is expanded or not, but whether or not a portion of the coracoscapular cartilage buds off and fuses to the first ray.

(89) P15 - narrow, elongate pec radials, with ventralmost expanded distally

0 - absent; 1 - present

(90) G19/ok34/in19 - actinosts (proximal pec radials) (unordered)

0 - four; 1 - seven or more; 2 - three

(91) pr19/G18/hmela3 - position of scapular foramen

0 - within scapula; 1 - between scapula and coracoid

Patterson and Rosen (1989: 15) note that this character was discovered by Cope (1872). According to Okamura (1970b:.94) there is variability in the position of the foramen in Bathygadidae. Okamura also describes the foramen as between the scapula and coracoid in *Brosme*, but it is within the scapula in *Lota* (Starks, 1930; Markle, 1989: 72; Howes, 1993: 23). Howes (1993: 23) states that the foramen is between the scapula and coracoid in most

supragadoids, which agrees with Markle's observations, but in his cladogram (figure 18) he places the character as diagnostic of gadiforms.

P12 - postcleithra

Postcleithra are lost in *Lophius* (Markle, 1989: 71), in carapids and most ophidiids (Markle and Olney, 1990: 285) and in some amblyopsids (Rosen and Patterson, 1969: table 1).

(92) jp19/ok29/in12 - position of first interneural spine

0 - between 4th and 5th neural spines or more posteriorly; 1 - between 3rd and 4th;
2 - between 2nd and 3rd; 3 - between 1st and 2nd; 4 - over so

According to Johnson and Patterson (1993: 606), in percopsids the first interneural spine lies posterior to the fourth neural spine, in *Aphredoderus* between the third and fourth, and anterior to the fourth in some ophidiiforms, some lophiiforms and many gadiforms. Howes (1993: 26-67) says that the position of the first interneural spine is very variable in ophidiiforms, anywhere between the first and the tenth vertebra, and is usually between the third and fourth in batrachoidiforms. He states that percopsids like *Melanonus* have the first interneural between the third and fourth vertebra. However, the illustration of *Melanonus* (figure 13C) shows the first interneural between the fourth and fifth vertebra, so I agree with Johnson and Patterson that the first interneural is behind the fourth in percopsids. Howes (p.27) observes that the first interneural in lophiiforms is placed between the eighth and ninth vertebra or even more posteriorly. This disagrees with Johnson and Patterson. In lophioid lophiiforms, which have an anteriorly placed first dorsal fin, the first interneural is placed anterior to the fourth. In carapids the first interneural appears always to lie posterior to the fourth vertebra (Patterson and Rosen, 1989: figures 9J, 9K; Markle and Olney, 1990: figures 2B-5). Markle and Olney (1990: 283) state that the origin of the first dorsal fin is posterior to the fourth vertebra in ophidiids and bythitids. However, as they show in their illustration, the first interneural spine in *Brotula* (figure 2A) is between the third and fourth neural spines. Johnson and Patterson (1993: 606) point out that the first interneural is anterior to the fourth vertebra in primitive zeiforms, beryciforms (their restricted sense, excluding stephanoberyciforms) and basal percomorphs, and they unite the three groups in an unnamed taxon. They note that anterior displacement occurs elsewhere in acanthomorphs, not only paracanthopterygians, in lampridiforms, Cretaceous polymixiids and one juvenile *Polymixia*, in a number of fossil groups possibly aligned with the acanthomorphs, namely Cretaceous ctenothrissiforms, Cretaceous aipichthyids, *Pharmacichthys* and *Pycnosteroides*. Posterior displacement is hypothesised to have happened independently several times, for example, in most smegmamorphs and gobioids. They note that the interneural spaces are not filled in these cases by

supraneurals, as in the primitive condition (e.g. ophidiiforms). Okamura (1989: 137) reports the position of the first interneural spine in the morid *Physiculus* as between the 4th and 5th neural spines. Elsewhere (Okamura, 1970b: table 17) he states that the first interneural is to be found between the second and third or third and fourth in morids. Markle (1982: figure 6B) shows the first interneural spine between the third and fourth vertebra in *Svetovidovia*. In the taxa omitted by Okamura, the states are as follows: in *Raniceps*, between third and fourth (Patterson and Rosen, 1989: figure 9H); in *Bregmaceros*, over the supraoccipital (Markle, 1982: figure 5D; Howes, 1993: 26); in the Gaidropsaridae, between first and second (Markle, 1982: figure 5B; Howes, 1993: 26); and in the Phycidae, between third and fourth (Markle, 1982: figure 5C; Patterson and Rosen, 1989: figures 9F, 9G).

(93) G24 - elongate 1D ray

0 - absent; 1 - present

Howes (1990: 91) argues that the condition in the Gaidropsaridae is not homologous with that in Bregmacerotidae and Muraenolepididae on the grounds of similarity: it is a 'specialised, vibratile structure, lying in a sensory groove and innervated by the facial nerve.' However, I do not see why this specialisation could not have occurred as a secondary modification. An elongate ray is also found in carapids and lophiiforms (Markle, 1989: 78).

(94) G26/27i - internal subdivision of 1D

0 - absent; 1 - present

I have lumped together and reorganised Markle's characters describing the numbers of dorsal fins in gadiforms. G27 describes the occasional absence of internal subdivision within the first dorsal fin, a condition covered by G26 (expressed here as G26/27i and subsuming ok3). G26 is meant also to describe internal subdivision within the second dorsal. However, it is not clear whether the taxa cited even have a second dorsal. This possibility is addressed by character G26/27ii which also expresses observations recorded in Svetovidov (1948) and Cohen *et al.* (1990). Iwamoto (1989: 168, iwa15) and Okamura (1989: 131, ok3) report that the Macrouroididae lack a second dorsal, and Inada (1989: 200, in8) reports that *Lyconus* does too.

(95) G26/27ii - 2D

0 - absent; 1 - present

A second dorsal fin is present in lophioid lophiiforms (Pietsch, 1984: table 88).

(96) P21 - number of elements in D and An radials

0 - two; 1 - three

(97) ha4/iwa17/ok4/in9 - fin spines in 1D

0 - two or more; 1 - one; 2 - none

Johnson and Patterson (1993: 599, jp1) consider 'azygous, unsegmented, bilaterally fused anterior fin-rays' to be a synapomorphy of acanthomorphs. Fin spines are lacking in the first dorsal of amblyopsids (Etnier and Starnes, 1993: 355, 356) and ophidiiforms (Cohen and Nielsen, 1978: 4) and are under reduction in the gadiforms.

(98) ok5 - relative development of D and An (unordered)

0 - D and An both short; 1 - D/2D long, better developed than short An; 2 - D/2D and An both long;

3 - An long, better developed than shorter 2D

The primitive state is taken from percopsiforms, in which dorsal and anal fins are both short (Wheeler, 1985: 282; Etnier and Starnes, 1993: 353, 355, 356). The third derived state is taken from Iwamoto and Sazonov (1988: figure 1). Data for those families not studied by Okamura are taken from Fahay and Markle (1984: tables 72, 75).

(99) ok6 - elevation of anterior portion of An

0 - absent; 1 - present

G21/in14/d*14 - number of precaudal v

A tendency to increase the number of precaudal vertebrae above 18 is found in a number of gadiform families, namely Moridae, Phycidae, Merlucciidae, Lotidae and Gadidae. I suggest that these tendencies are expresses independently in each family.

(100) pr17i/G32/hmela13/ok1/ok2/in10 - C

0 - present; 1 - absent

Markle (1989: 81) reports Macrouridae (theoretically including Bathygadidae, Trachyrincidae and Macrouroididae) and Steindachneriidae as tailless, and the caudal fin of *Macruronus* as 'very diminutive'. Inada (1989: 202) describes loss of the caudal fin in *Steindachneria*, *Lyconus* and *Macruronus*. Okamura (1989: 131) prefers to present this character as a matter of degree. He describes the caudal fin of *Macruronus* and *Lyconus* as considerably reduced. Cohen *et al.* (1990:

90) state that *Trachyrincus* does indeed have a caudal fin, and Howes (1989: figure 6) illustrates its caudal skeleton. The caudal fin is absent in carapids (Fujita, 1990: figures 147, 148).

(101) pr17ii/P22/G29/hmacn4/hmela15/d4 - X and Y bones

0 - absent; 1 - present

Patterson and Rosen (1989) present X and Y bones as a synapomorphy of the gadiforms as a whole. However, Markle (1989: 81) reports X and Y lost in Melanonidae, Lotidae and Gadidae.

(102) G30/d28 - total number of C rays

0 - low, less than 45; 1 - moderate to high, between 46 and 70

Markle (1989: 81) reports very high numbers of caudal fin rays in melanonids, lotids and gadids. Low numbers are found in the gadids *Gadiculus* and *Trisopterus* (Dunn, 1989: 230).

G31 - procurrent C rays

Markle (1982: figure 7C; Fahay and Markle, 1984: 281) defines the primary (principal) caudal fin rays as those inserting on the upper hypurals, counting those inserting on the lower hypurals and parhypural as secondary (procurrent) caudal rays. This usage is unconventional and does not correspond with that employed by Johnson and Patterson (1993: 616) for example, where principal caudal rays include those on upper and lower hypurals including the parhypural. Markle (1989: 81) cites Fahay and Markle (1984) for a distinct asymmetry in procurrent caudal rays in morids and euclichthyids. However, Fahay and Markle (1984: 282) state that 'Morids are the only group of tailed gadiforms that show noticeable asymmetry in superior versus inferior secondary [procurrent] caudal rays.' In their table 76, *Euclichthys* does not show a significant asymmetry, having 17 procurrent caudal rays in the upper lobe and 16 in the lower lobe, if one is subtracted for the parhypural. Markle (1982: 3430) states that 'The external asymmetry of caudal fin rays in *Svetovidovia* ... is atypical of gadoids but appears characteristic of a few morids. Normally, the difference in gadoid procurrent rays (superior minus inferior) is -4 to +1 while in the morids examined it is -9 to -2.' Asymmetries calculated from corrected counts of procurrent rays (based on Fahay and Markle, 1984: table 76, and Fujita, 1990: figures 137, 138) are between -4 and +4 for morids and -3 and +3 in other gadiforms. Morids may show a tendency to greater asymmetry, but this is no means consistently expressed and does not appear to exist in *Euclichthys*.

(103) G33/hmacn8/hmela16 - fused upper hypural

0 - absent; 1 - present

No paracanthopterygian has more than five hypurals and all have a lower hypural plate except morids (Fujita, 1990: figures 136-156), although a bone that may be identified as the 'sixth' hypural is present in percopsiforms. Upper hypural plates are present in amblyopsids, aphredoderids, ophidiiforms, pediculates and most gadiforms. Johnson and Patterson (1993: 613, jp28) give five or fewer hypurals as a synapomorphy of percomorphs, noting independent acquisition in melamphaeids and berycids. They miss the homoplasy in paracanthopterygians. This is strange since Rosen and Patterson (1969: 365-366) describe reduction of the number of hypurals to five as a widespread feature of acanthomorphs including paracanthopterygians. They even illustrate upper and lower hypural plates in *Percopsis* (figure 16A). Howes (1990: 89) cites a fused upper hypural as a character defining a group of 'higher gadoids', in which he includes the Ranicipitidae, but this is contradicted by the observations of Dunn and Matarese (1984: 287, 299; figure 148B) namely that the upper hypurals are not fused. (Note that Dunn and Matarese label the parhypural as the first hypural.) Fusion of the upper hypurals is variable in *Euclichthys polynemus* (compare Markle, 1989: figures 16 and 17A). Howes (1993: 30, figures 15A, 15B) notes an 'almost complete' upper hypural plate in *Melanonus*, with the hypurals fused distally, and contrasts this with the situation in morids. However, those morids illustrated by Fujita (1990: figures 137, 138) have two or three of the upper hypurals fused distally.

(104) jp33/G35 - number of principal C rays

0 - 18; 1 - between 10 and 12; 2 - less than 10

Johnson and Patterson (1993: 616) describe 17 or fewer principal caudal rays as a synapomorphy of percomorphs (including atherinomorphs), independently acquired in zeiforms. However, Gill (in press) notes that less than 17 rays are found in higher paracanthopterygians. Fujita (1990) illustrates 12 principal caudal rays in batrachoidids (figure 150) and less than 10 in ophidiids (figures 143, 146), bythitoids (figures 144, 145, 149) and lophiiforms (figures 151-156). Numbers of principal caudal rays are adjusted (see above) from Fahay and Markle (1984: table 76) and Dunn and Matarese (1984).

(105) G34/d*40 - neural and haemal arches of more than ten caudal v in association with the support of procurrent C rays

0 - less than 10; 1 - more than 10

(106) hmacn5/hmela13 - *interradiales* connecting C rays with D and An rays

0 - absent; 1 - present

The linkage pattern of the *interradiales* is absent in *Trachyrincus* (Howes, 1991a: figure 35) and *Melanonus* (Howes, 1993: 26) in common with other paracanthopterygians.

(107) ns1i - sulcus type (unordered)

0 - homosulcoid; 1 - heterosulcoid; 2 - archaesulcoid

Nolf and Steurbaut's (1989c) otolith characters are adjusted to fall in line with the otolith terminology of Smale *et al.* (1995) and data on ophidiiforms and pediculates are taken from there (pp. 65-70). Nolf and Steurbaut (1989a: 40-41, figures 6C, 6D) provide data on percopsiforms. Smale *et al* (1995: figure 8) describe the different sulcus types. Percopsiform, carapid and batrachoidid otoliths are homosulcoid, like the majority of gadiforms. Ophidiids have heterosulcoid otoliths, as do morids. Bythitoid, lophiiform, trachyrincid and macrouroidid otoliths are archaesulcoid.

(108) ns1ii - pince-nez sulcus

0 - absent; 1 - present

The pince-nez sulcus is a variety of the homosulcoid type.

(109) ns2 - raised collicula

0 - absent; 1 - present

Raised collicula are found in carapids, bythitoids, some ophidiids and lophiiforms, and most gadiforms except bregmacerotids, muraenolepidids and gaidropsarids.

(110) ns3 - elongation of otoliths

0 - absent; 1 - present

Elongate otoliths are present in carapids, some ophidiids and lophiiforms.

ns4 - bulging inner face; ns5 - blunt ventral rim

These two characters are recorded by Nolf and Steurbaut (1989c: figure 13) in phycids and gadids. However, among gadids they occur only in *Trisopterus* (Nolf and Steurbaut, 1989c: 102, 108), which is not even thought to be the most primitive genus (see Dunn, 1989: figure 29).

(111) nsa1 - crista inferior enlarged

0 - no; 1 -yes

Enlargement of the crista inferior occurs in carapids and some batrachoidids.

nsa2 - *Nezumia*-like pattern

'The pattern of adult *Nezumia* is found in juveniles of many other genera, whose juvenile otoliths cannot be distinguished from those of *Nezumia* ... we can conclude that ancestral macrourine otoliths must have been close to the morphology of present-day *Nezumia* ...' (Nolf and Steurbaut, 1989c: 95, 92). In their diagram of relationships, Nolf and Steurbaut (1989c: figure 13) describe a *Nezumia*-like pattern as linking macrourids *sensu stricto*, trachyrincids and macrouroidids. However, the pattern in trachyrincids and macrouroidids (figure 5) is very different, being archaesulcoid.

(112) nsa3 - central part of collicula depressed

0 - no; 1 - yes

The central part of the collicula is depressed in batrachoidids.

(113) nsa4 - otoliths moderate to thin, lateral surface flat to concave

0 - no; 1 - yes

Some bythitoids have thin, flat otoliths.

(114) ha5 - reticulate scales

0 - absent; 1 - present

In his discussion of macrourid scale types, Okamura (1970b: 12) observes reticulate scales in some species of the genus *Nezumia*, namely *N. condylura*, *N. kamoharai*, *N. proxima* and *N. tomiyamai*.

(115) ok7/iwa11 - scales

0 - cycloid; 1 - peripheral ctenoid

This character is also discussed by Howes (1989: 123). Peripheral ctenoid scales are present in percopsids and aphredoderids (Rosen and Patterson, 1969: table 1). Transforming ctenoid scales are unique to percomorphs (Johnson and Patterson, 1993: 614, jp30), although absent in atherinomorphs, gasterosteiforms, synbranchiforms and tetraodontiforms (see Roberts, 1993, for definitions of scale types).

(116) Howes (1991a: 99) - RLA nerve

0 - present; 1 - absent

Howes admits that a wider survey of this character is needed.

(117) ok22 - precranial cavity

0 - present; 1 - reduced or absent

ok23 - anterior position of olfactory bulbs

According to Howes (1989: 123) an anterior shift of the olfactory bulbs is not restricted to gadiforms and may have been independently derived a number of times. Fahay (1989: 156) suggests the position of the olfactory bulbs is a secondary effect of the extent of the precranial cavity. Little agreement is found in the states assigned to the different families by Marshall and Cohen (1973: 485), Howes (1989: 123), Okamura (1989: 135, ok23) and Fahay (1989: 156). The Trachyrincidae, Macrouroididae and certain Macrouridae are unanimously ascribed a position near the forebrain. In these the precranial cavity is reduced or absent (see ok22, above).

(118) G20/iwa22 - position of anus

0 - abdominal, close to A origin; 1 - abdominal, removed from A origin; 2 - thoracic

The anus is thoracic in aphredoderids and amblyopsids (Rosen, 1985: 43) and carapids (Markle and Olney, 1990: 283).

(119) ok38/d*42 - anterior processes on swimbladder

0 - absent; 1 - present

Details for gadiform families not covered by Okamura (1989) are provided by Svetovidov (1948). Okamura (1989: 137) claims that the swimbladder is lost in *Squalogadus* and *Melanonus*, but Howes (1993: 28) confirms its presence in *Melanonus*.

(120) G37/ok38/iwa23 - light organs

0 - absent; 1 - present

Markle (1989: 82) states that light organs are found in the Euclichthyidae, Steindachneriidae, Macrouridae *sensu lato* and Moridae. Okamura (1989: 138) confirms the report of a light organ in *Euclichthys* and *Steindachneria* (Cohen, 1964). They are present in many of the Macrouridae *sensu stricto*, but absent in Bathygadidae, Trachyrincidae and Macrouroididae. Paulin (1989: table 1) reports a light organ only in the *Physiculus* subgroup of the Moridae. Light organs are present in some batrachoidids (Wheeler, 1985: 132).

Chapter 4.3: Results of Analysis

Complete data for the 120 characters are analysed using the mh* bb* option in Hennig86, using a hypothetical taxon of all plesiomorphic states as the outgroup. Two trees result, length 427, CI 0.39, RI 0.63 (Figure 54A). With regard to paracanthopterygians as a whole, the concepts of Aphredoderoidei, Anacanthini and Pediculati supported by Patterson and Rosen (1989) are corroborated. However, their doubts concerning the integrity of the Percopsiformes, Ophidiiformes and Ophidioidei are not justified here and each is confirmed as monophyletic. The sister group relationship between the Pediculati and the Gadiformes proposed by Patterson and Rosen appears in one of the two trees. However, in the other tree, the Ophidiiformes is the sister group of the Gadiformes, resulting in Gadiformes *sensu* Greenwood *et al.* (1966), although excluding the zoarcids.

The resulting classification of the Gadiformes is very similar to that of Howes (1993). Three suborders are recognised, Melanonoidei, Macrouroidei and Gadoidei. The Melanonidae is more basal than macrouroids and gadoids, as first proposed by Markle (1989). The Macrouroidei is that implied by Howes (1990, 1991b) and consists of the Trachyrincidae and Macrouridae *sensu* Howes (1988, 1989), namely Macrouroidinae plus Macrourinae.

Howes' placement of the Bathygadidae, Moridae, *Steindachneria* and *Euclichthys* as 'infragadoids' is supported. Instead of forming a paraphyletic group (Howes, 1989, 1990, 1991a), they are a monophyletic group, the Moroidea. Howes (1993) uses this name for a taxon co-ordinate with the Gadoidea (supragadoids), which, following Markle (1989), comprises the Euclichthyidae plus the Moridae. The Bathygadidae and Steindachneriidae were placed as *incertae sedis* within the Gadoidei. I am now able to resolve the position of these two families. Okamura (1989) and Inada (1989) accept Marshall's (1966) alignment of *Steindachneria*, *Macruronus* and *Lyconus* with *Merluccius* and surprisingly this arrangement is supported here. *Steindachneria* belongs to an infragadoid family, as suggested by Howes, but that family does not exclude *Macruronus*, *Lyconus* and *Merluccius*. *Macruronus* and *Lyconus* are not basal supragadoids as argued by Markle (1989) and Howes (1991a). The Moridae are the sister group to the Merlucciidae *sensu lato*, and the Bathygadidae is the sister group to these two. The Bathygadidae therefore does belong with the macrouroids, the traditional view supported by Nolf and Steurbaut (1989c), Okamura (1989) and Iwamoto (1989; but see Sazonov and Iwamoto, 1992).

Markle (1989) places *Raniceps* as more basal than *Melanonus*, but here *Raniceps* is placed within a traditional Gadidae (see Cohen *et al.*, 1990), close to the forked hakes. As indicated by Howes (1989) and formalised in Howes (1991b), the rocklings form a group distinct from the forked hakes. They are placed as the basal subfamily, Gaidropsarinae, of the Gadidae *sensu lato*. The Phycinae and Gadinae are sister groups, and each consists of two tribes, Ranicipitini and Phycini, Lotini and Gadini respectively. The Bregmacerotidae and Muraenolepididae are placed in basal suborders by Nolf and Steurbaut (1989c), following the tradition of Svetovidov (1948). This arrangement is not corroborated here. Both belong to the Gadoidea, the Muraenolepididae being the sister group of the Gadidae and the Bregmacerotidae the sister group of the two. Except for the Merlucciidae *sensu lato*, the Gadoidea is equivalent to the Gadoidei of Markle (1989) and to the Gadoidea (supragadoids) of Howes (1993).

The classification below is derived from a strict consensus of the two trees resulting from the Hennig86 analysis (Figure 54B), using a sequencing convention. Following Wiley (1981), each taxon is listed as the sister group of all others at the same rank (indicated by the same indentation). *Sedis mutabilis*, meaning of changeable position, is used to denote polytomies.

Paracanthopterygii
- Percopsiformes
  - Percopsoidei
    - Percopsidae
  - Aphredoderoidei
    - Aphredoderidae
    - Amblyopsidae
- Anacanthini
  - Ophidiiformes *sedis mutabilis*
    - Ophidioidei
      - Carapidae
      - Ophidiidae
    - Bythitoidei
  - Pediculati *sedis mutabilis*
    - Lophiiformes
    - Batrachoidiformes
  - Gadiformes *sedis mutabilis*

Melanonoidei

Melanonidae

Macrouroidei

Trachyrincidae

Macrouridae *sensu lato*

Macrouroidinae

Macrourinae

Gadoidei

Moroidea

Euclichthyidae

Bathygadidae

Moridae

Merlucciidae *sensu lato*

Steindachneriinae

Macruroninae

Merlucciinae

Gadoidea

Bregmacerotidae

Muraenolepididae

Gadidae *sensu lato*

Gaidropsarinae

Phycinae

Ranicipitini

Phycini

Gadinae

Lotini

Gadini

Character diagnoses follow for each of the groups recognised in the classification. I have listed parallelisms and subsequent reversals for any characters where they occur.

A. Percopsiformes

A1. Three elements in dorsal and anal fin radials, 96 (1); also in Batrachoidiformes

A2. Six branchiostegal rays, 54 (1); also in some Macrourinae

A3. Ossified supraneurals, both ends enclosed in bone, 79 (2)

B. Aphredoderoidei

B1. Segmented premaxilla, 26 (1)

B2. Fused upper hypural, 103 (1); also in Anacanthini

B3. Thoracic anus, 118 (2); also in Carapidae

C. Anacanthini

C1. Posterior myodome, 16 (1); also in Amblyopsidae

C2. "Gadoid notch", 27 (1), lost in Melanonidae

C3. Second centrum, or second and third, foreshortened, much shorter than first and third or fourth, 80 (1)

C4. First parapophysis at fourth vertebra or more posteriorly, 81 (1), at third in Bregmacerotidae

C5. Pelvic fin rays reduced to six or fewer, 86 (1), reversed in Moroidea minus Euclichthyidae, and some Melanonidae, Trachyrincidae, Macrouridae, Bregmacerotidae, Gaidropsarinae, Lotini and Gadini

C6. Dorsal fins long, 98 (1)

C7. Fewer than 18 principal caudal rays, 104 (1)

D. Ophidiiformes

D1. Nasals lost, 1 (2); also in Pediculati

D2. Ethmoid cartilage forms vertical plate behind mesethmoid, 7 (1); also in Macrouroidei, Moroidea and Muraenolepididae

D3. Supraoccipital excluded from border of foramen magnum, 23 (1); also in Melanonidae and some Macrourinae

D4. A1b divided into medial and lateral components, 43 (1)

D5. Complex strut joint between anterior ceratohyal and hypohyals, 52 (1); also in Percopsidae and Pediculati

D6. Two branchiostegal rays on posterior ceratohyal, 55 (1); also in Trachyrincidae, Macrouroididae and some Lophiiformes

D7. Interarcual ligament lost, 57 (1); also in Trachyrincidae, Macrourinae, some Merlucciinae and Gadoidea (except Ranicipitini)

D8. *Rectus communis* inserts on anterior tip of urohyal, 68 (1), reversed in some Ophidiidae; also in Muraenolepididae, Phycinae and Lotini

D9. First neural spine reduced, 74 (1)

D10. Exoccipital condyles displaced forward from of basioccipital condyle, with corresponding extension of "prezygapophyses", 77 (1); also in Gadiformes

D11. Pleural ribs short, rod-like, 83 (1); also in Melanonidae, Merluciidae *sensu lato*, Gaidropsarinae, Ranicipitini and Lotini

D12. Baudelot's ligament originates on the occiput, 87 (1); also in Batrachoidiformes

D13. Dorsal spiny rays lost, 97 (2); also in Amblyopsidae and Gadiformes

D14. Fewer than 10 principal caudal fin rays, 104 (2); also in Trachyrincidae, Muraenolepididae plus Gadidae *sensu lato* and some Lophiiformes

D15. Otoliths have raised collicula, 109 (1); also in Gadiformes and some Lophiiformes

E. Ophidioidei

E1. Interarcual cartilage large, 56 (2); also in Melanonidae

E2. Swimbladder ligamentously connected to anterior ribs, 85 (1)

F. Pediculati

F1. Nasals lost, 1 (2); also in Ophidiiformes

F2. Sphenotic enlarged, flaring laterally 14 (2)

F3. Intercalar lost, 21 (1)

F4. Posttemporal fused to skull, 24 (1)

F5. Infraorbital series reduced, 25 (2)

F6. Partially or completely independent ascending process of premaxilla, 28 (1)

F7. Entopterygoid lost, 30 (1); also in Bregmacerotidae

F8. Complex strut joint between anterior ceratohyal and hypohyals, 52 (1); also in Percopsidae and Ophidiiformes

F9. "Bear's paw" third pharyngobranchial, 62 (1); also in Gadiformes

F10. First neural spine immovably fused to supraoccipital, 73 (1) Pediculati; also in Bythitoidei, Melanonidae, Merlucciidae *sensu lato* and some Gadidae *sensu lato*

F11. Exoccipital facets "cod-like", 78 (1); also in Gadiformes

F12. Pleural ribs absent, 82 (1)

F13. Narrow, elongate pectoral radials, with ventralmost expanded distally, 89 (1)

G. Gadiformes

G1. Foramina for cranial nerves absent from prootic, 17 (1); also in some Bythitoidei

G2. Small lower window, 37 (1), lost in Macrouroidinae

G3. Part or all of A1b in same plane as A1a, 41 (1), reversed in Euclichthyidae, Macruroninae and Muraenolepididae plus Gadidae *sensu lato*

G4. A1/A1b attaches medially to maxilla, 46 (1)

G5. *Levator arcus palatini* partially or wholly lateral to adductor complex, 47 (1), medial in Trachyrincidae and Muraenolepididae plus Gadidae *sensu lato*)

G6. *Adductor arcus palatini* inserts posteriorly, 49 (1), reversed in Moroidea; also in some Ophidiiformes

G7. Ligamentous coupling between opercular series and lower jaw involves hyomandibula and preoperculum, 50 (1), reversed in Macrouridae *sensu lato*; also in Bythitoidei

G8. First pharyngobranchial cartilaginous or lost, 60 (1), ossified in Euclichthyidae and Steindachneriinae; also in Carapidae, Lophiiformes and some Batrachoidiformes

G9. "Bear's paw" third pharyngobranchial, 62 (1); also in Pediculati

G10. Reduction of *obliqui ventrales* on first arch, 64 (1), reversed in Macrouridae *sensu lato* and Euclichthyidae

G11. *Retractor dorsalis* inserts on third pharyngobranchial only, 71 (1), on third and fourth in Merlucciinae and Gadidae *sensu lato*, on fourth only in Muraenolepididae

G12. Subsequent neural spines shortened, 76 (1) , reversed in Macrouroidinae and Gadini

G13. Exoccipital condyles displaced forward from of basioccipital condyle, with corresponding extension of "prezygapophyses", 77 (1); also in Ophidiiformes

G14. Exoccipital facets "cod-like", 78 (1); also in Pediculati

G15. First parapophysis at fifth vertebra or more posteriorly, 81 (2), at fourth in Moridae and Gadoidea

G16. Epineurals absent from first vertebra, 84 (1); also in Lophiiformes

G17. Dorsal spiny rays absent, 97 (2), present in Moroidea; also in Amblyopsidae and Ophidiiformes

G18. Pince-nez sulcus 108 (1)

G19. Raised collicula, 109 (1), concave in Gadoidea; also in Ophidiiformes and some Lophiiformes

H. Macrouroidei plus Gadoidei

H1. Palatine forming hinge or butt joint with pterygoids, 29 (1); also in Percopsidae

H2. A1a and whole of A1b lie in same plane, 41 (2), reversed in Merlucciidae *sensu lato* and Gadidae *sensu lato*

H3. A1/A1b originates from preopercular limb, or from a fascia of A2 or the *levator arcus palatini,* 45 (1), from hyomandibula in Gadidae *sensu lato*

H4. Insertion of A1/A1b on dorsomedial ledge or ventromedial process, 46 (2), on medial aspect of head in Merlucciidae *sensu lato*, laterally in Muraenolepididae plus Gadidae *sensu lato*)

H5. Second dorsal fin, 95 (1), lost in Macrouroidinae and some Macruroninae and Lotini; also in some Lophiiformes

J. Macrouroidei

J1. Large nasals, 1 (1)

J2. Ethmoid cartilage forms vertical plate behind mesethmoid, 7 (1); also in Ophidiiformes, Moroidea and Muraenolepididae

J3. Vomerine teeth absent, 13 (1); also in Percopsidae, Euclichthyidae, Bathygadidae and Muraenolepididae

J4. Stout *sternohyoideus* associated with urohyal widely separated from pelvic girdle, 70 (1), reversed in some Macrourinae

J5. Central part of collicula depressed, 112 (1), reversed in some Macrourinae; also in Batrachoidiformes, Moridae and Bregmacerotidae

J6. Peripheral ctenoid scales, 115 (1); also in Percopsidae and Aphredoderidae

J7. Precranial cavity reduced or absent, 117 (1)

K. Macrouridae *sensu lato*

K1. V-Y shaped crest, 3 (1); also in Batrachoidiformes, Moroidea and Muraenolepididae

K2. Foramen for mandibular branch of hyomandibular facial nerve absent, 40 (1); also in Melanonidae and Steindachneriinae

K3. Ligamentous coupling between opercular series and lower jaw does not involve in hyomandibula and preoperculum, 50 (0)

K4. *Obliqui ventrales* on first arch complete, 64 (0); also in Euclichthyidae

K5. Anterior neural spines enlarged, 74 (2); also in Melanonidae, Moroidea, Muraenolepididae and Gadinae

K6. First interneural spine between second and third neural spines, 92 (2); also in Gadoidei

K7. Caudal fin lost, 100 (1); also in Carapidae, Bathygadidae and Steindachneriinae

L. Gadoidei

L1. Palatine contacts ethmovomerine bloc, ten (1), reversed in Bathygadidae and Steindachneriinae

L2. Ectopterygoid reduced, 32 (1); also in Merlucciinae

L3. Articular surface of second pharyngobranchial strut-like, contacts distal tip of first epibranchial, 61 (1), contacts uncinate process in Bathygadidae, Steindachneriinae and Macruroninae; also in Bythitoidei and Macrouroidinae

L4. *Rectus communis* attaches to dorsal surface of *sternohyoideus*, 68 (2), attaches to urohyal in Muraenolepididae, Phycinae and Lotini

L5. Scapular foramen between scapula and coracoid, 91 (1), within scapula in Steindachneriinae and some Bathygadidae and Lotini

L6. First interneural spine between second and third neural spines, 92 (2), between third and fourth in Phycinae and Gadini; also in Macrouridae *sensu lato*

L7. X and Y bones, 101 (1), lost in Macruroninae and Gadinae

L8. *Interradiales* connect caudal fin rays to dorsal and anal rays, 106 (1)

M. Moroidea

M1. V-Y shaped crest, 3 (1) Moroidea; also in Batrachoidiformes, Macrouroidei and Muraenolepididae

M2. Ethmoid cartilage forms vertical plate behind mesethmoid, 7 (1) Moroidea, reversed in Merlucciidae; also in Ophidiiformes, Macrouroidei and Muraenolepididae

M3. A1b incompletely divided, 42 (1) Moroidea, reversed in Bathygadidae plus Moridae plus Merlucciidae *sensu lato*

M4. Tendinous constriction of A1b, 44 (1) Moroidea; also in Melanonidae

M5. Anterior insertion of *adductor arcus palatini*, 49 (0) Moroidea, posterior in Merlucciidae *sensu lato*)

M6. Interarcual cartilage small, 56 (1) Moroidea, lost in some Merlucciinae

M7. Ligamentous connection between first and second epibranchial, 59 (0) Moroidea; also in Batrachoidiformes, Melanonidae, Macrouroidinae and Gadidae *sensu lato*

M8. Two or more spinous rays in first dorsal fin, 97 (0) Moroidea, one in Merlucciinae and some Macruroninae

N. Bathygadidae plus Moridae, Merlucciidae *sensu lato*

N1. A1 divided, 42 (0); also in Gadidae *sensu lato*

N2. *Sternohyoideus* long, compressed, 69 (1), short in Steindachneriinae; also in some Ophidiidae and Bythitoidei

N3. Pelvic fins with more than six rays, 86 (0), fewer than six in some Moridae; also in some Melanonidae, Trachyrincidae, Macrouridae, Bregmacerotidae, Gaidropsarinae, Lotini and Gadini

P. Moridae plus Merlucciidae *sensu lato*

P1. Contact between lateral ethmoid and palatine narrow, 12 (1); also in Melanonidae

P2. *Obliqui ventrales* on second gill arch weak, 65 (1); also in Melanonidae and Gadini

P3. Direct connection between swimbladder and vertebral column, 85 (2); also Bythitoidei and Phycinae plus Gadinae

P4. Otoliths elongate, 110 (1); also in Carapidae, Gadidae *sensu lato*, and some Ophidiidae, Lophiiformes, Bathygadidae and Macrourinae

P5. Anterior processes on swimbladder, 119 (1), absent in some Macruroninae; also in Gadidae *sensu lato*

Q. Merlucciidae *sensu lato*

Q1. A1b medial to A1a, 41 (1)

Q2. A1b constricted and preorbitally expanded, 44 (2); also in Gadidae *sensu lato*

Q3. A1b originates from medial aspect of head, 46 (1)

Q4. Posterior insertion of *adductor arcus palatini*, 49 (1)

Q5. *Rectus ventralis IV* inserts on dorsal aponeurosis of *sternohyoideus*, 66 (2), reversed in Macruroninae; also in Lotini

Q6. First centrum fused to exoccipital and basioccipital condyles, 72 (1); also in Melanonidae

Q7. First neural spine immovably fused to supraoccipital, 73 (1); also in Bythitoidei, Pediculati, and Gadidae *sensu lato*

Q8. Pleural ribs short, rod-like, 83 (1); also in Ophidiiformes, Melanonidae, Gaidropsarinae, Ranicipitini and Lotini

Q9. Thin, flat otoliths, 113 (1); also in Melanonidae, Muraenolepididae, Phycini and some Bythitoidei

R. Macruroninae plus Merlucciinae

R1. Deep fossa within pterosphenoid, sphenotic and pterotic accommodating sixth infraorbital, 15 (1); also in Lotidae

R2. Prootic with transverse septum, 20 (1)

R3. Symplectic process of preoperculum contacts symplectic cartilage, 35 (1)

R4. Large lower window, 37 (2); also in Gadinae

R5. Entire A1b medial to A1a, 41 (0); also in Gadidae *sensu lato*

R6. *Rectus communis* attaches to *sternohyoideus* via tendinous aponeurosis, 68 (4)

R7. RLA nerve lost, 116 (1)

S. Gadoidea

S1. Lateral ethmoid palatine ligament lost, 11 (1); also in Merlucciinae

S2. Contact between lateral ethmoid and palatine broad, 12 (2); also in Merlucciinae

S3. Thin walled prootic with deeply indented notches for optic and trigeminal nerves, 18 (2), reversed in Phycinae; also in Steindachneriinae and Merlucciinae

S4. Supraoccipital crest reduced, 22 (1), reversed in Phycini and Gadini

S5. Upper window present, 36 (1); also in Melanonidae, Moridae and Merlucciinae

S6. Interarcual ligament absent, 57 (1), present in Ranicipitini; also in Ophidiiformes, Trachyrincidae, Macrourinae and some Merlucciinae

S7. First parapophysis at fourth or more posteriorly, 81 (1), at third in Bregmacerotidae

S8. Elongate first dorsal fin ray, 93 (1), reversed in Phycinae plus Gadinae; also in Carapidae and Lophiiformes

S9. Concave collicula, 109 (0), raised in Muraenolepididae plus Gadidae *sensu lato*

T. Muraenolepididae plus Gadidae *sensu lato*

T1. Firm articulation between first infraorbital and lateral ethmoid wing, 9 (1); also in Merlucciinae

T2. Symplectic triangular to oblong, no stem, 34 (1); also in Merlucciinae

T3. Symplectic process of preoperculum contacts lateral face of hyomandibula, 35 (2), contacts symplectic head in Ranicipitini and Lotini

T4. A1b originates laterally, on ventral limb of maxillary head, 46 (0)

T5. *Levator arcus palatini* medial to adductor complex, 47 (0), partially lateral in Ranicipitini

T6. Joint between posterior ceratohyal and interoperculum, 53 (1); also in Batrachoidiformes, Trachyrincidae and Macrouroidinae

T7. Uncinate process absent on first epibranchial, 58 (1), present in Ranicipitini

T8. Fewer than ten principal caudal fin rays, 104 (2), more than ten in Phycini

T9. Raised collicula, 109 (1)

U. Gadidae *sensu lato*

U1. Contact between lateral ethmoid and parasphenoid very broad, 12 (3)

U2. Preopercular process of hyomandibula, 38 (1); also in Merlucciinae

U3. Entire A1b medial to A1a, 41 (0); also in Macruroninae plus Merlucciinae

U4. A1 divided, 42 (0); also in Moroidea minus Euclichthyidae

U5. Constriction and preorbital expansion of A1b, 44 (2); also in Merlucciidae *sensu lato*

U6. A1b originates from hyomandibula, 45 (0)

U7. Ligamentous connection between first and second epibranchial, 59 (0); also in Batrachoidiformes, Melanonidae, Macrouroidinae and Moroidea

U8. *Retractor dorsalis* inserts on third and fourth pharyngobranchial, 71 (1); also in Merlucciinae

U9. First neural spine immovably fused to supraoccipital, 73 (1); also in Bythitoidei, Pediculati and Merlucciidae *sensu lato*

U10. Second dorsal and anal fin equally developed, 98 (2); also in Merlucciidae and Bregmacerotidae

U11. Otoliths elongate, 110 (1); also in Carapidae, Moridae plus Merlucciidae *sensu lato*, and some Ophidiidae, Lophiiformes, Bathygadidae and Macrourinae

U12. Anterior processes on swimbladder, 119 (1), absent in Ranicipitini; also in Moridae plus Merlucciidae *sensu lato*

V. Phycinae plus Gadinae

V1. Direct connection between swimbladder and vertebral column, 85 (2); also in Bythitoidei and Moridae plus Merlucciidae *sensu lato*

V2. Elongate first dorsal fin ray lost, 93 (0)

W. Phycinae

W1. Trigeminal notch in sagittal plane, prootic wall thickened posterior to notch, 18 (1)

W2. *Rectus ventralis IV* inserts on urohyal, 66 (1); also in Muraenolepididae

W3. *Rectus communis* inserts on urohyal, 67 (0); also in Lotini

W4. *Rectus communis* inserts on anterior tip of urohyal, 68 (1); also in Ophidiiformes, Muraenolepididae and Lotini

W5. Supraneurals ossified, ends tipped with cartilage, 79 (1); also in Euclichthyidae

W6. First interneural spine between third and fourth neural spines, 92 (1); also in Aphredoderidae, Batrachoidiformes, Trachyrincidae and Gadini, and some Ophidiidae and Lophiiformes

X. Gadinae

X1. Wide separation between body and process of quadrate, 33 (1); also in Muraenolepididae

X2. Large lower window, 37 (2); also in Macruroninae plus Merlucciinae

X3. Preopercular process ventrally directed, 39 (1); also in Merlucciinae

X4. No branchiostegal rays on posterior ceratohyal, 55 (2); also in Trachyrincidae and Macrouroidinae

X5. First parapophysis at fifth vertebra, 81 (2)

X6. X and Y bones lost, 101 (0); also in Macruroninae

X7. Total number of caudal fin rays high, 102 (1); also in Melanonidae

X8. Neural and haemal arches of more than ten caudal vertebrae in association with the support of procurrent caudal fin rays, 105 (1); also Melanonidae and Merlucciidae

Chapter 4.4: Ecological Scenarios

Howes (1988, 1989) proposes a scenario that there are two feeding strategies among gadiform fishes, namely protrusion and precision. Protrusion feeders are typified by the Macrouridae and Macrouroididae and throw the jaw forward in a somewhat imprecise fashion. The supragadoids, on the other hand, adopt restricted but more precise jaw movements, which may still involve protrusion. Howes (1989) considers the polarity to be from protrusibility to precision, and converts the functional scenario into a historical scheme. The family Macrouridae (comprising Macrourinae plus Macrouroidinae) is taken to be the sister group of all other gadiforms. The infragadoids are interpreted as stages in the acquisition of the supragadoid jaw precision system.

Five myological characters from the WOGADS data set contribute to the feeding strategy, namely h1/9, h3, h5, h11, h12 and h18. Okamura (1970b) relates jaw protrusion in macrouroids to the relative length of premaxillary ramus and I have taken data for this character from the rattail analysis. The characters are listed below with the transformation series polarised according to the scenario of Howes (1989), precision to protrusion. The implication of this scenario, given the resulting cladogram, can be summarised by considering an index of protrusion/precision derived from the six characters. For simplicity the index is calculated according to Howes' polarity, so that high values represent precision feeding, low values represent protrusion. The values are normalised so that each character contributes equal information and the index varies between 0 and 1. For taxa where the genera are known to differ, namely Macrourinae and Macruroninae, the value of the character taken for the index is the average of the extreme values. Values of the index for Gaidropsarinae, Phycini, Ranicipitini, Lotini and Gadini are identical and the five families are treated as Gadidae *sensu lato*.

(gad41) h1/9 - plane of A muscles

0 - elements lie in same plane; 1 - anterior part of A1b medial with respect to other elements;

2 - entire A1b medial with respect to other elements

Casinos (1981) states 'that the restriction A1b to the same vertical plane as A1a gives the upper jaw a degree of freedom greater than that of gadoids where the vertical movement of the maxilla appears to be restricted by the obliquely and transversely angled A1b ...' (Howes, 1988: 51-52).

(gad50) h3 - ligamentous coupling between opercular series and lower jaw

0 - op-sop-iop; 1 - op/sop/pop/hyo-iop

Howes (1989: 126) interprets the presence of a direct interopercular-preopercular-hyomandibula coupling in gadoids as part of a general amplification of biomechanical pathways and components that has taken place above the macrouroids, related to an increase in the manipulative functions of the upper jaw (Howes, 1988: 60).

(gad42) h5 - A1

0 - undivided; 1 - incompletely divided into A1a and A1b; 2 - divided into A1a and A1b;

3 - divided into A1a, A1b and A1c

Division of the muscle amplifies jaw precision by increasing the number of separately acting biomechanical components.

(gad45) h11 - origination of A1b

0 - posteriorly;1 - anteriorly, from pal

Restricted, precise jaw movement reaches an extreme in merlucciids where the short A1b affords the maxilla little downward movement (Howes, 1988: 52).

(gad46) h12 - site of attachment of muscle A1/A1b to m

0 - ventromedial process; 1 - dorsomedial ledge; 2 - medial aspect of head; 3 - ventral limb of head

Insertion of A1b further forward on the maxilla restricts the degree of jaw protrusibility (Howes, 1988: 38, 52). In forms with higher jaw precision, the ventromedial process of the maxilla is less prominent. The most derived condition is where the ventromedial process is reduced to a medial shelf and A1b inserts at the symphysial border of the maxillary head. The anterior shift of A1b is correlated with the medial shift and enlargement of the whole muscle, allowing greater jaw precision (Howes, 1988: 39, 52).

(macr18) length of premaxillary ramus by height of ascending process

0 - 225%; 1 -116-118%; 2 - 93%; 3 - 82-85%; 4 - 70%; 5 - <=62%

	gad41	gad50	gad42	gad45	gad46	macr18	Index
Melanonidae	1	1	2	0	2	5	0.64
Trachyrincidae	0	1	0	0	1	5	0.39
Macrouroidinae	0	0	0	0	?	4	0.16
Macrourinae	0	0	2	0	0	2.5	0.19
Euclichthyidae	2	1	1	0	1	5	0.61
Moridae	0	1	2	0	0	5	0.44
Bathygadidae	0	1	2	0	0	5	0.44
Steindachneriinae	1	1	1	0	2	5	0.58
Macruroninae	2	1	1.5	1	2	5	0.86
Merlucciinae	2	1	2	1	2	5	0.89
Bregmacerotidae	2	1	0	0	1	5	0.56
Muraenolepididae	2	1	0	0	3	5	0.67
Gadidae *s.l.*	2	1	2	0	3	5	0.78

In the following table the protrusion/precision index is compared with the depth range for each of the 13 taxa. The depth data are taken from Cohen *et al.* (1990) and Howes (1991b) and given in kilometres. The values of the index and the depths are ranked and ranks are listed alongside the corresponding raw values. Spearman rank correlation coefficients are calculated for the pairwise comparisons between the index and depth from the formulae given in Siegel (1956).

	Index	rank	Min depth	rank	Max depth	rank
Melanonidae	0.64	10	0.1	6.5	3	10
Trachyrincidae	0.39	3	0.4	11	2.5	8
Macrouroidinae	0.16	1	0.2	9.5	5.3	12
Macrourinae	0.19	2	0.1	6.5	6.5	13
Euclichthyidae	0.61	8	0.6	12.5	0.9	3.5
Moridae	0.44	4.5	0.2	9.5	3	10
Bathygadidae	0.44	4.5	0.1	6.5	3	10
Steindachneriinae	0.58	6	0.6	12.5	0.9	3.5
Macruroninae	0.86	12	0.05	4	0.65	2
Merlucciinae	0.89	13	0.02	3	2	7
Bregmacerotidae	0.56	7	0	1.5	0.3	1
Muraenolepididae	0.67	9	0.1	6.5	1.6	5.5
Gadidae *s.l.*	0.78	11	0	1.5	1.6	5.5

The Spearman rank correlation coefficient between the protrusion/precision index and minimum depth is -0.542, significant at $p<0.05$. Between protrusion/precision index and maximum depth the rank correlation coefficient is -0.578, significant at $p<0.025$. Significance is judged on the t distribution, degrees of freedom $N - 2 = 11$, using a one-tailed test (Siegel, 1956). The significant negative correlations mean that a lower index is associated with higher minimum and maximum depths and a higher index is associated with lower minimum and maximum depths.

Within the framework of relationships justified here, each suborder and superfamily can be seen to have its own tendency to diverge from the primitive paracanthopterygian value, which is 0.44. The macrouroids have high jaw protrusibility, showing much lower values of the index, and range to great depths, to the continental rise and abyss. The infragadoids (Moroidea) tend to have values around the paracanthopterygian level and live on the continental slope. The morids and bathygadids have lower values, towards greater jaw protrusion, and *Euclichthys* and *Steindachneria* have higher values, towards greater jaw precision. The macruronines and the merlucciines are exceptional, however. They have the highest jaw precision of any gadiform and extend on to the continental shelf. The supragadoids (Gadoidea) are shelf dwellers and characteristically have high jaw precision. *Bregmaceros* and *Muraenolepis* have lower values compared to gadids (*sensu lato*) but still above the primitive paracanthopterygian value. Light does not penetrate into the continental rise and abyss and light levels are highest on the continental shelf. High jaw precision may therefore imply visual predation. High jaw protrusibility may be an advantage where the prey cannot be visualised exactly, and the jaw is thrown forward in response to non-visual cues.

Chapter 5: Scenarios and Relationships of Gadiform Fishes II

Rattail Systematics

Chapter 5.1: Results of Analysis

Wilson (1994) provides the most up-to-date review of the systematics of the *Coryphaenoides* group, summarising conclusions from peptide mapping and allozyme data. However, he complains (p. 48) that 'there has been no rigorous phylogenetic study of *Coryphaenoides (s. l.)* based on morphology to which to compare these results.' I now provide that comparison and adopt the same total evidence approach that I employed in the WOGADS synthesis. I incorporate Wilson's data, as far as it is compatible, with my own derived from observations of the head skeleton of rattails. Wilson's (1994) allele frequency data are not compatible with the matrix of discrete morphological characters, but the peptide mapping data of Wilson, Siebenaller and Davis (1991) are.

Wilson *et al.* (1991) compared homologues of muscle type lactate dehydrogenase by trypsin digestion. A data matrix was prepared for nine species of *Coryphaenoides (s. l.)* and one species of *Caelorinchus* by pairwise comparison of the chromatograms. The matrix consists of the presence or absence of 56 peaks, corresponding to presence or absence of particular peptides. The analysis was performed using the Wagner parsimony algorithm in PHYLIP 3.1. Wilson *et al.* fix *Caelorinchus occa* as the root of their trees. They are therefore unable to comment on the integrity of *Coryphaenoides*. Wilson (1994: 49) comments on the difficulty of deciding on the position of the root, and with a restricted set of species returns only 2 trees (Wilson, 1994: figures 2B, 2C). I have selected the 34 informative characters from those provided by Wilson and colleagues (Wilson *et al.*, 1991: table 1; Wilson, 1994: table 4; see Table 3). Analysis of these characters with ie* in Hennig86 results in two trees, length 65, CI 0.52, RI 0.51. If rooted at *Caelorinchus occa* these equal the first two trees obtained by Wilson *et al.* (1991: figures 4A, 4B; see Figure 55A). However, this rooting is not the only possible. I have also investigated the effect of rooting at *Albatrossia pectoralis* (Figure 55B). It is surprising that Wilson did not contemplate this arrangement, having discussed Iwamoto and Sazonov's (1988) proposal that its separate generic status be upheld. The significance of this alternative rooting becomes clear when the total evidence is analysed.

A single tree results from mh* bb* analysis of the morphological data alone, length 255, CI 0.40, RI 0.64 (Figure 56). The morphological tree is compatible only with the first protein tree. The

total evidence, morphological and molecular, is recorded in Table 4. Three trees result from mh* bb* analysis in Hennig86, length 321, CI 0.42, RI 0.63 (Figure 57A; consensus, Figure 57B). Again, they are compatible only with the first protein tree. Including the morphological data resolves the disagreement between the two significantly different topologies allowed in the analysis of peptide mapping data alone. Since I have scored a wider range of rattail species for morphology, the problem of rooting is solved through the inclusion of the morphological data.

Two grade are usually recognised among rattails, those with seven branchiostegal rays versus those with six. Okamura (1970b) distinguishes these as the *Nezumia* group and the *Caelorinchus* group. Iwamoto (1977) indicates three subgrades of the seven-rayed species, which are roughly followed by Okamura. *Hymenocephalus* forms a distinct line, next come *Echinomacrurus*, *Cetonurus*, *Mataeocephalus*, *Sphagemacrurus* and *Trachonurus*, and the most derived group comprises *Malacocephalus*, *Ventrifossa* and *Nezumia*. Iwamoto (also Iwamoto, 1972) names the last line the Malacocephalini. My analysis confirms the paraphyletic, grade-like nature of the *Nezumia* group and Iwamoto's three subgrades are roughly represented. *Hymenocephalus* forms the basal macrourine genus and the Malacocephalini, here revised to include *Trachonurus* as well, is the sister taxon to the Macrourini or *Caelorinchus* group. In between *Echinomacrurus*, *Mataeocephalus*, *Cetonurus* and *Sphagemacrurus* are arranged in a comb. This arrangement is only provisional and awaits a study aimed specifically at the seven branchiostegal ray species.

Iwamoto and Sazonov (1988) provide the most up-to-date cladogram of the relationships of the six-rayed species. A number of important conclusions from that paper are corroborated here. *Albatrossia pectoralis* is the basal species of the *Coryphaenoides* group on the basis of having only 2 retia mirabilia in the swimbladder. *Lionurus* plus *Chalinura* and *Nematonurus* and *Caelorinchus* plus *Macrourus* are corroborated and belong within *Coryphaenoides* group. The distinctiveness of the type species *Coryphaenoides rupestris*, indicated by Iwamoto and Stein (1974), is given some support. A number of species traditionally assigned to *Coryphaenoides* are more closely related to *Caelorinchus* and *Macrourus* than they are to their type species, namely *Coryphaenoides guentheri*, *C. mexicanus*, *C. anguliceps*, *C. cinereus* and *C. zaniophorus*. I have described these species, along with *Caelorinchus* and *Macrourus*, as the *Coryphaenoides zaniophorus* alliance. Such an alliance is hinted at by Wilson *et al.* (1991) in their peptide mapping results. The disagreement between the three total evidence trees lies within the *Coryphaenoides zaniophorus* alliance, with regard to the placement of *C. anguliceps* and *C. cinereus*. They lie between *C. mexicanus* and *C. zaniophorus* but there their position cannot be resolved further. Only morphological data are available for *C. anguliceps* and only published data

are available for *C. cinereus*. The disagreement between the three trees represents lack of information, rather than conflicting information.

The classification below is based on a strict consensus of the three trees resulting from the Hennig86 analysis (Figure 57B). The classification is derived from the consensus diagram using the same sequencing convention as that used in the previous chapter. Following Wiley (1981), each taxon is listed as the sister group of all others at the same rank (indicated by the same indentation). *Sedis mutabilis* is used to denote polytomies.

Macrourinae

- *Hymenocephalus*
- *Echinomacrurus*
- *Mataeocephalus*
- *Cetonurus*
- *Sphagemacrurus*
- Malacocephalini
  - *Nezumia*
  - *Trachonurus*
  - *Malacocephalus*
  - *Ventrifossa*
- Macrourini
  - *Albatrossia*
  - *Coryphaenoides* (*Macrourus* and *Caelorinchus* as subgenera)
  - *Lionurus*
  - *Chalinura*
  - *Nematonurus*

The classification of the genus *Coryphaenoides* poses special problems for nomenclature. The solution I have chosen is to expand the genus to include *Macrourus* and *Caelorinchus* as subgenera. It is unlikely that this nomenclatural difficulty will be avoided after further work, because of the likelihood that *Coryphaenoides* is indeed paraphyletic with respect to *Caelorinchus* and *Macrourus*. The binomials of the species of the genera need not be altered if we adopt the interpretation of the Code proposed by Disney (1989). There it is suggested that the first name of a binomial in a case such as this may be the name of a subgenus. This avoids continuing to name groups shown to be paraphyletic by new research, but preserves nomenclatural stability. An undesirable effect is that *Macrourus*, the type of its tribe, subfamily, family and suborder, does not

appear in the classification as a full genus. If this is thought unwelcome then the scope of the genus *Macrourus* may be made equal to what I have described below as the *Coryphaenoides zaniophorus* alliance. The former species of *Coryphaenoides* would be classified as species of *Macrourus*, subgenus unspecified; species of *Macrourus* and *Caelorinchus* as specified subgenera of the expanded genus. I leave it to the reader to decide which option he finds more appropriate.

Coryphaenoides

Coryphaenoides rupestris alliance

Coryphaenoides rupestris

Coryphaenoides acrolepis

Coryphaenoides filifer

Coryphaenoides zaniophorus alliance

Coryphaenoides guentheri

Coryphaenoides mexicanus

Coryphaenoides anguliceps sedis mutabilis

Coryphaenoides cinereus sedis mutabilis

Coryphaenoides zaniophorus

Coryphaenoides (Macrourus)

Coryphaenoides (Macrourus) berglax

Coryphaenoides (Caelorinchus)

Coryphaenoides (Caelorinchus) caelorhincus

Coryphaenoides (Caelorinchus) occa

A. *Echinomacrurus* plus *Mataeocephalus*, *Cetonurus*, *Sphagemacrurus*, Malacocephalini, Macrourini

A1. Medial process of palatine, 27 (1), reversed in *Trachonurus villosus* and *Lionurus*

A2. 46 (1), lost in *Echinomacrurus mollis*

A3. Posterior lamina of interhyal not extended, 53 (1), *Trachonurus villosus* and *Coryphaenoides*

A4. First hypobranchial short, 57 (1), reversed in *Malacocephalus laevis*

A5. *Rectus communis* fully attached to *sternohyoideus*, 84 (1), inserts on the urohyal in *Ventrifossa sp.* and *Nezumia aequalis*

A6. Dentition heterodont, 86 (1)

B. *Mataeocephalus* plus *Cetonurus*, *Sphagemacrurus*, Malacocephalini, Macrourini

B1. Mesethmoid swells around ethmoid cartilage where latter articulates with lateral ethmoid, 5 (1), lost in all species of Macrourini examined, except *Macrourus berglax*

B2. Dorsal concavity of interoperculum, 46 (1)

B3. Head of fourth branchiostegal ray expanded, with notch in posterior surface, 55 (1), notch lost in *Sphagemacrurus hirundo*

B4. Lamina produced from whole of proximal perichondral ossification of second hypobranchial, 59(1), reversed *Coryphaenoides zaniophorus* alliance

B5. Serrated spinous first dorsal fin ray, 74 (1), smooth in *Trachonurus villosus*, *Malacocephalus laevis* and *Caelorinchus*

C. *Cetonurus* plus *Sphagemacrurus*, Malacocephalini, Macrourini

C1. Light organ present, 77 (2), lost in Macrourini; also in *Hymenocephalus italicus*

D. *Sphagemacrurus* plus Malacocephalini, Macrourini

D1. Ascending process of premaxilla low, 18 (0), increases in height within *Coryphaenoides mexicanus* plus *Coryphaenoides anguliceps*, *Coryphaenoides cinereus*, *Coryphaenoides zzaniophorus*, *Macrourus* and *Caelorinchus*; also in *Hymenocephalus italicus*

D2. Ventral process of first epibranchial, 64 (1), lost in *Coryphaenoides guentheri* and *Coryphaenoides zaniophorus* plus *Macrourus* and *Caelorinchus*

D3. Toothplate not fused to third epibranchial, 68 (1), fused in *Nezumia aequalis*

E. Malacocephalini plus Macrourini

E1. Interdigitation between anterior and posterior ceratohyals lost, 50 (1), regained in *Trachonurus villosus* and *Caelorinchus* plus *Macrourus*; also in *Melanonus zugmayeri*

E2. Lateral surface of anterior ceratohyal tucked in anterodorsally to meet dorsal hypohyal, 51 (1), reversed *Trachonurus villosus* and *Chalinura*

E3. Jaws small, mouth inferior, 71 (1), reversed in *Malacocephalus* plus *Ventrifossa* and *Chalinura*; also in *Echinomacrurus mollis* and *Mataeocephalus microstomus*

E4. Lamina produced well from whole of proximal perichondral ossification of second hypobranchial, 75 (1)

E5. First adductor muscle fully divided, 85 (1), reversed in *Malacocephalus* plus *Ventrifossa*

F. Malacocephalini

F1. Entopterygoid pentagonal, 32 (1); also in *Mataeocephalus microstomus*

F2 Strong central protuberances of preoperculum, 42 (1), lost in *Ventrifossa sp.*; also in *Mataeocephalus microstomus*

F3 Anal and urogenital openings encircled by broad band of naked black skin situated far from anal fin origin, 70 (1)

G. *Trachonurus* plus *Malacocephalus* and *Ventrifossa*

G1. Rounded processes on mesethmoid for ethmo-maxillary ligaments, 4 (1)

G2. Ascending process of first infraorbital strong, 12 (0); also in *Melanonus zugmayeri*, *Cetonurus globiceps*, *Coryphaenoides anguliceps*, *Coryphaenoides zaniophorus*, *Macrourus berglax*, and *Lionurus* plus *Chalinura* and *Nematonurus*

G3. Scale patches on gular membrane, 80 (1), lost in *Nezumia aequalis*; also in *Melanonus zugmayeri*, *Cetonurus globiceps* and *Coryphaenoides rupestris*

H. *Malacocephalus* plus *Ventrifossa*

H1. Two pairs of horizontal lateral flanges, 7 (0); also in *Melanonus zugmayeri*

H2. Lateral shelf extends posteriorly beyond posterior perichondral ossification, posterior portion embayed, 29(1)

H3. Process of ectopterygoid contacts perichondral ossification of palatine, 34 (1); also in all species of Macrourini examined

H4. First hypobranchial bears ventral process, 58 (1)

H5. Jaws large, mouth subterminal, 71 (0)

H6. First adductor muscle incompletely divided, 85 (0)

J. Macrourini

J1. Six branchiostegal rays, 54 (1)

J2. Light organ lost, 77 (0); regained in *Macrourus* plus *Caelorinchus*; also in *Echinomacrurus* and *Mataeocephalus*

K. *Coryphaenoides* plus *Lionurus*, *Chalinura* and *Nematonurus*

K1. 4 or more retia mirabilia, 75 (1); also in *Melanonus zugmayeri*.

L. *Coryphaenoides* (including *Macrourus* and *Caelorinchus* as subgenera)

L1. Nasals fused or closely adjoined, 1(1)

L2. Palatine process of ectopterygoid significantly expanded medially, 35 (1); reversed in *Macrourus* plus *Caelorinchus*

L3. Notch in ventral surface of hyomandibula, 40 (1), lost in *Coryphaenoides anguliceps* and *Caelorinchus caelorhincus*; also in *Mataeocephalus microstomus*, *Malacocephalus laevis*, *Chalinura brevibarbis* and *Nematonurus armatus*

L4. Posterior lamina of interhyal extended ventrally, 53 (0)

L5. Interior perichondral ossification of dorsal hypohyal regained, 52 (0), lost again in *Macrourus* and *Caelorinchus*

L6. Vagal lobes of brain well-developed, mouth and pharynx richly covered in taste buds, 72 (1), reversed in *Macrourus berglax*; also in *Nezumia*

L7. Peptide peak 31 lost, 101 (0), regained in *Coryphaenoides zaniophorus*

L8. Peptide peak 37 lost, 104 (0), regained in *Caelorinchus occa*

L9. Peptide peak 54, 118 (1), lost in *Coryphaenoides acrolepis*

M. *Lionurus* plus *Chalinura*, *Nematonurus*

M1. Wide mesethmoid process of lateral ethmoid, 6 (0); also in *Melanonus zugmayeri* and *Cetonurus globiceps*

M2. Balloon-shaped basioccipital, 10 (1)

M3. Ascending process of first infraorbital strong, 12 (0); also in *Melanonus zugmayeri*, *Cetonurus globiceps*, *Trachonurus* plus *Malacocephalus* and *Ventrifossa*, *Coryphaenoides anguliceps*, *Coryphaenoides zaniophorus* and *Macrourus berglax*

M4. Posteroventral extension and crest of fifth infraorbital lost,13 (1)

M5. Weak lateral shelf of palatine, 30 (0); also in *Melanonus zugmayeri*, *Malacocephalus laevis* and M6. 5-7 retia mirabilia, 75 (2)

M7. Entopterygoid rectangular, 31 (1); also in *Sphagemacrurus hirundo*, *Echinomacrurus mollis* and *Coryphaenoides anguliceps*

M8. Anterior strut of hyomandibula large, 39 (1); Also in *Coryphaenoides anguliceps*

M9. Elongate interoperculum, 45 (1); also in *Mataeocephalus microstomus* and *Coryphaenoides zaniophorus* plus *Macrourus* and *Caelorinchus*

M10. Ventral concavity of interoperculum, 48 (1); lost in *Chalinura brevibarbis*; also in *Mataeocephalus microstomus* and *Caelorinchus* plus *Macrourus*

M11. Swimbladder does not drumming muscles in either sex, 73 (0); also in *Melanonus zugmayeri*

M12. Naked areas either side of snout, 81 (1); also in *Cetonurus*, *Caelorinchus caelorhincus* and *Macrourus berglax*

M13. Underside of snout naked or sparsely scaled, 82 (1); also in *Coryphaenoides guentheri* and *Caelorinchus* plus *Macrourus*

N. *Lionurus*

N1. Medial process of palatine lost, 27 (0)

N2. Palatine boss high and narrow, set at large angle to prong, 28 (1)

N3. Lateral flange of preoperculum large, poorly ossified, 43 (2)

N4. Interoperculum posteriorly club-shaped, 47 (1); also in *Mataeocephalus microstomus*, *Chalinura brevibarbis*, *Coryphaenoides mexicanus*, *Coryphaenoides zaniophorus*, *Macrourus* plus *Caelorinchus*

N5. Narrow ventral process of first epibranchial, 67 (1)

P. *Chalinura* plus *Nematonurus*

P1. Perichondral ossification forms most of posterior border of retroarticular, 24 (1); also in *Mataeocephalus microstomus* and *Echinomacrurus mollis*

Q. *Chalinura*

Q1. Downward extension of nasals shallow, 2 (0); Also *Melanonus zugmayeri*

Q2. Fifth infraorbital flat and anvil-shaped, 15 (1)

Q3. Anterior ceratohyal no longer tucked in anterodorsally to meet dorsal hypohyal, 51 (0)

Q4. Jaws large, mouth subterminal, 71 (0)

R. *Nematonurus*

R1. Lateral flange of preoperculum large and roof-like, 43 (2)

LA. *Coryphaenoides rupestris* alliance

LA1. Peptide peak 43, 110(1)

LB. *Coryphaenoides acrolepis* plus *Coryphaenoides filifer*

LB1. Peptide peak 42, 109 (1); also in *Albatrossia pectoralis*

LB2. Peptide peak 49 lost, 115 (0); also in *Coryphaenoides cinereus*

LC. *Coryphaenoides zaniophorus* alliance

LC1. Anterior ceratohyal broad, 49 (1); also in *Mataeocephalus microstomus*.

LC2. Base of urohyal very broad, crest very prominent distally, posterodorsal process pointed, 56 (2)

LC3. Lamina produced only from part of proximal perichondral ossification of second hypobranchial, 59 (0); reversed in *Caelorinchus* plus *Macrourus*

LC4. No toothplate fused to third epibranchial, 68 (1)

LD. *Coryphaenoides mexicanus* plus *Coryphaenoides anguliceps*, *Coryphaenoides cinereus*, *Coryphaenoides zaniophorus*, *Coryphaenoides (Macrourus)*, *Coryphaenoides (Caelorinchus)*

LD1. High ascending process of premaxilla, 18 (1)

LD2. Weak lateral shelf of palatine, 30 (0); also in*Melanonus zugmayeri*, *Malacocephalus laevis* and *Lionurus* plus *Chalinura* and *Nematonurus*

LE. *Coryphaenoides anguliceps*, *Coryphaenoides cinereus* plus *Coryphaenoides zaniophorus*, *Coryphaenoides (Macrourus)*, *Coryphaenoides (Caelorinchus)*

LE1. Mesethmoid processes for ethmo-maxillary ligament stubby, 4 (2); also in *Coryphaenoides rupestris*

LE2. First infraorbital long, 11 (0), moderate in *Caelorinchus caelorhincus*; also in *Melanonus zugmayeri*, *Cetonurus globiceps*, *Trachonurus* plus *Malacocephalus* and *Ventrifossa*, and *Lionurus* plus *Chalinura* and *Nematonurus*

LE3. Boss of bone on retroarticular acting as site of attachment for mandibular-interopercular ligament lost, 26 (0); also in *Hymenocephalus italicus*, *Echinomacrurus mollis*, *Sphagemacrurus hirundo*, *Lionurus carapinus*, *Coryphaenoides rupestris*

LE4. Peptide peak 28, 99 (1); also in *Chalinura leptolepis*

LE5. Peptide peak 29, 100 (1)

LE6. Peptide peak 44, 111 (1); also in *Coryphaenoides filifer*

LE7. Peptide peak 50 lost, 116 (0); also in *Coryphaenoides acrolepis* and *Coryphaenoides filifer*

Coryphaenoides zaniophorus plus *Coryphaenoides (Macrourus)*, *Coryphaenoides (Caelorinchus)*

LF1. Pterosphenoid extended ventrally, 8 (1); also in *Chalinura leptolepis*, *Nematonurus armatus* and *Nematonurus yaquinae*

LF2. Degree of overlap between exoccipitals short, 9 (1); also in *Lionurus filicauda*, *Chalinura* and *Nematonurus*

LF3. Sixth infraorbital a narrow, deep channel, 16 (1); also in *Mataeocephalus microstomus* and *Malacocephalus laevis*

LF4. Increase in height of ascending process of premaxilla, 18 (2)

LF5. Low postmaxillary process of premaxilla, 19 (1); also in *Mataeocephalus microstomus*

LF6. Notch in posterolateral portion of maxilla small, 22 (0)

LF7. Slope of retroarticular well anteroventral, 23 (1); also in *Coryphaenoides guentheri*

LF8. Thin plate of hyomandibula lost, 41 (1)

LF9. Lateral flange of preoperculum projects backwards, 43 (1); also in *Coryphaenoides guentheri*

LF10. Interoperculum elongate, 45 (1); also in*Mataeocephalus microstomus* and *Lionurus* plus *Chalinura* and *Nematonurus*

LF11. Ventral process of first epibranchial lost, 64 (0); also in *Melanonus zugmayeri*, *Hymenocephalus italicus*, *Cetonurus globiceps*, *Mataeocephalus microstomus* and *Coryphaenoides guentheri*.

LF12. Peptide peak 1, 87 (1)

LF13. Peptide peak 3, 88 (1)

LF14. Peptide peak 27, 98 (1); also in *Chalinura leptolepis*

Coryphaenoides (Macrourus) plus *Coryphaenoides (Caelorinchus)*

LG1. Fifth infraorbital a deep channel, 14 (2); also in *Mataeocephalus microstomus*

LG2. Increase in height of ascending process of premaxilla, 18 (4)

LG3. Short postmaxillary process of premaxilla, 20 (0); also in *Melanonus zugmayeri* and *Mataeocephalus microstomus*

LG4. Arch between head and articular process of maxilla, 21 (1)

LG5. Medial expansion of palatine process of ectopterygoid negligible, 35 (0)

LG6. Area of contact between posterior process of quadrate and preoperculum very broad, 38 (1); also in *Mataeocephalus microstomus*

LG7. Ventral concavity of interoperculum, 48 (1); also in *Mataeocephalus microstomus* and *Lionurus* plus *Chalinura* and *Nematonurus*

LG8. Interdigitation between anterior and posterior ceratohyals regained, 50 (1)

LG9. Interior perichondral ossification of dorsal hypohyal lost, 52 (1)

LF10. Lamina produced from whole of proximal perichondral ossification of second hypobranchial,
59 (1)

LG11. Process on first ceratobranchial, 61 (1)

LG12. Process on third ceratobranchial, 62 (1)

LG13. Large distal lamina of first epibranchial, 65 (1)

LG14. Outer gill rakers on first arch absent, 76 (1); also in *Mataeocephalus microstomus*

LG15. Light organ regained, at least in rudimentary form, 77 (1)

LG16. Underside of snout naked or sparsely scaled, 82 (1); also in *Lionurus* plus *Chalinura* and *Nematonurus*, and *Coryphaenoides guentheri*

Coryphaenoides (Caelorinchus)

LH1. Smooth spinous first dorsal fin ray, 74 (0); also in *Hymenocephalus*, *Echinomacrurus*, *Malacocephalus* and *Trachonurus*

LH2. Light organ fully re-established, 77 (2)

Chapter 5.2: Ecological Scenarios

A value of a precision/protrusion index for each species is calculated in the same way as in the previous chapter. The values are tabulated below.

Species	gad42	macr18	Index
Hymenocephalus italicus	1	5	0.22
Echinomacrurus mollis	1	3	0.16
Mataeocephalus microstomus	1	0	0.06
Cetonurus globiceps	1	3	0.16
Sphagemacrurus hirundo	1	5	0.22
Nezumia aequalis	3	5	0.33
Trachonurus villosus	2	5	0.28
Malacocephalus laevis	1	5	0.22
Ventrifossa sp.	1	5	0.22
Lionurus filicauda	3	5	0.33
Lionurus carapinus	3	5	0.33
Chalinura leptolepis	3	5	0.33
Chalinura brevibarbis	3	5	0.33
Nematonurus armatus	3	5	0.33
Nematonurus yaquinae	3	5	0.33
Coryphaenoides rupestris	3	5	0.33
Coryphaenoides guentheri	3	5	0.33
Coryphaenoides mexicanus	3	3	0.27
Coryphaenoides anguliceps	3	4	0.3
Coryphaenoides zaniophorus	3	2	0.23
Caelorinchus caelorhincus	3	1	0.2
Macrourus berglax	2	1	0.14

In the following table the protrusion/precision index is compared with the depth range for each of the 22 species. Minimum and maximum depths are taken from Marshall (1973), Iwamoto and Sazonov (1988), and Endo and Okamura (1992) and are given in kilometres. The values of the index and the depths are ranked and ranks are listed alongside the corresponding raw values. Spearman rank correlation coefficients are calculated for the pairwise comparisons between the index and depth from the formulae given in Siegel (1956).

Species	Index	rank	Min depth	rank	Max depth	rank
Hymenocephalus italicus	0.22	6.5	0.1	1.5	0.8	2
Echinomacrurus mollis	0.16	6.5	0.5	10.5	2.3	13
Mataeocephalus microstomus	0.06	2.5	5	22	5.413	21
Cetonurus globiceps	0.16	2.5	0.96	16	2	10
Sphagemacrurus hirundo	0.22	1	0.4	8.5	1.1	6
Nezumia aequalis	0.33	6.5	0.2	5.5	1	4
Trachonurus villosus	0.28	6.5	0.2	5.5	1.5	7
Malacocephalus laevis	0.22	18	0.2	5.5	1	4
Ventrifossa sp.	0.22	11.5	0.5	10.5	1.6	8.5
Lionurus filicauda	0.33	4	0.2	5.5	0.5	1
Lionurus carapinus	0.33	11.5	0.1	1.5	1	4
Chalinura leptolepis	0.33	18	0.18	3	2.2	12
Chalinura brevibarbis	0.33	18	2.47	20	5.07	20
Nematonurus armatus	0.33	18	0.61	12	4	18
Nematonurus yaquinae	0.33	18	2	19	4.7	19
Coryphaenoides rupestris	0.33	18	0.831	15	2.83	16
Coryphaenoides guentheri	0.33	18	1.4	17	2.8	15
Coryphaenoides anguliceps	0.3	18	1.5	18	3.2	17
Coryphaenoides mexicanus	0.27	18	4.1	21	6.45	22
Coryphaenoides zaniophorus	0.23	9	0.4	8.5	2.165	11
Caelorinchus caelorhincus	0.2	10	0.73	14	1.6	8.5
Macrourus berglax	0.14	13	0.722	13	2.418	14

The Spearman rank correlation coefficient between the protrusion/precision index and minimum depth is 0.280, significant at $p>0.10$. Between protrusion/precision index and maximum depth the rank correlation coefficient is 0.507, significant at $p<0.05$. Significance is judged on the *t* distribution, degrees of freedom $N - 2 = 20$, using a one-tailed test (Siegel, 1956). The sign of the correlations between depth and the protrusion/precision index is now positive, rather than negative as for the suborder Macrouroidei. This suggests a reversal of the overall direction of evolutionary change within the Macrourinae, from precision to protrusion to protrusion to precision. This may be described as a form of mosaic evolution. Variations running counter to the theme are able to exploit new niches, since these organisms possess novel combinations of characters.

Mostly, the observed species with seven branchiostegal rays are characterised by jaw protrusion and those with six branchiostegal rays by jaw precision. Exceptions are *Trachonurus* and *Nezumia*, of the Malacocephalini, which link the tribe to the sixes by their increased jaw precision. *Caelorinchus* and *Macrourus* are linked with species of the genus *Coryphaenoides* which show increasing jaw protrusion, namely *C. anguliceps*, *C. mexicanus* and *C. zaniophorus*. It is interesting to note that, in common with the species with seven branchiostegal rays, *Caelorinchus* possesses a light organ, and *Macrourus* shows a rudimentary organ, whereas in the rest of the *Coryphaenoides* group luminescence is absent.

The three genera *Lionurus*, *Chalinura* and *Nematonurus* comprise abyssal species, but have a relatively high jaw precision. Unlike *Echinomacrurus* and the macrouroidids, which are also deep living, the swimbladder is not regressed. In fact retial lengths are very high. This allows a very high pressure to be built up in the swimbladder and thus the typical macrourid swimming mode of hovering above the substrate is still possible even at this great depth. The number of retia is also increased. *Chalinura* and *Lionurus* particularly have soft bones and small eyes, reductions suitable to the deep water habitat. I have indicated in the list of characters that the three genera do not have a well-developed gustatory system, compared to *Nezumia*, *Coryphaenoides* and *Caelorinchus*, where the mouth and pharynx are richly endowed with taste buds. Nor does either sex have drumming muscles attached to the swimbladder. It may seem something of a mystery how these fishes communicate with each other and how they find prey animals (see Marshall, 1971). However, fishes living this deep are unlikely to be using smell to hunt prey, since this is a time and energy consuming business. *Echinomacrurus* and the macrouroidids have a well-developed acoustico-lateralis system, with wide, mucus-filled canals. Observations of the canal bones in *Lionurus*, *Chalinura* and *Nematonurus* suggest that they too have a better developed lateral line system. Characters of the fifth and sixth infraorbitals show that the canal in these three genera is more open, the crests on either side of the canal poorly developed. In the species of *Chalinura* the nasal bones are flat and open, and the fifth infraorbitals are wide and anvil-shaped. *Chalinura* is also distinguished by a subterminal mouth, unique amongst the *Coryphaenoides* group. Everything points to these three genera being a specialised radiation of rattails that has moved to the abyss from the continental slope. This is direction of dispersal that Wilson (1994: 49) thinks most likely and is implicit in the conclusions of Iwamoto and Sazonov (1988). *Lionurus*, *Chalinura* and *Nematonurus* fail to show what Howes (1989) viewed as the typical macrourid hyomandibula, where the anterior strut of the bone has undergone attrition. The anterior strut has enlarged again even though the mandibular branch of the facial nerve does not perforate it. Here is another example of a mosaic of primitive and derived states.

Chapter 6: The Role of Secondary Cartilage in the Development of Dermal Bones in Rattails

Chapter 6.1: Introduction

The seminal discussion by Patterson (1977) provides the framework for this chapter. Without his account the observations recorded here would not derive as much importance. It is therefore necessary to review his claims. Patterson (1977: 79) identifies three classes of bone. A cartilage bone is a bone preformed in cartilage, which may develop membranous outgrowths. A dermal bone is a bone not preformed in cartilage, associated with the ectoderm or topographically homologous to a bone that is so associated. A membrane bone ossifies deep in the mesoderm, with no connection with the ectoderm. It is homologous with a cartilage bone, but is no longer preformed in cartilage. The vertebrate exoskeleton consists of a single class, the dermal bones, and the endoskeleton consists of the cartilage bones plus the membrane bones.

Patterson's claim is that cartilage in the exoskeleton is restricted to birds and mammals (Patterson, 1977: 88-92). However, when discussing the possibility of cartilage in the exoskeleton of actinopterygians, Patterson only considers reported cases of former dermal bones now represented in the dermal skeleton solely as cartilages (Patterson, 1977: 89-91). He does not address the far more interesting question of whether cartilage is ever involved in the development of dermal bones. Patterson refers to the cartilaginous subopercular of the amblyopsid *Typhlichthys subterraneus* reported by Rosen (1962: figure 16), but does not acknowledge Rosen's observation of cartilaginous portions of the other opercular bones (see figure 16 for *Typhlichthys subterraneus* and figure 5 for the fellow amblyopsid *Chologaster agassizi* and the distantly related esociform *Umbra limi*). These observations are willingly explained away, indeed by Rosen himself in a personal communication to Patterson, as simply indicating poorly ossified or membranous regions of bone. Indeed to say that the distribution of cartilage as indicated by Rosen (1962) is identical to that in rattails (according to the figures of Okamura, 1970b, and my personal observations) and other paracanthopterygians (Rosen and Patterson, 1969: figures 8 and 9) is still to rely on circumstantial evidence. The question that must be asked is how could poorly ossified bone be distinguished from cartilage. Patterson's discussion appears in the same year as a protocol for the differential staining of cartilage and bone (Dingerkus and Uhler, 1977). I have used this protocol to make observations that support the existence of cartilage in the exoskeleton of fishes. Dunn (1983: 2) briefly discusses some problems with the Dingerkus-Uhler method of staining. His own personal

observations and those of D. W. Nelson, communicated to him, reveal that certain ossified structures may stain blue, namely 'teeth, spines and rays, and scutes'. Nonetheless, alcian blue is generally accepted as a critical means of staining cartilage in contrast to bone in whole mounts (e.g. Hall, 1986; Taylor, Hall, Miyake and Cone, 1994).

Moss and Moss-Salentijn (1983) provide a summary of vertebrate cartilage from the point of view of a histologist. Moss and Moss-Salentijn argue for a modulation theory of the skeleton, stating 'that all vertebrate skeletal tissues form a continuous spectrum and that all skeletal tissue types are produced by cytodifferentiating modulation of a common stem-cell scleroblast' (Moss and Moss-Salentijn, 1983: 4). Rightly, they see the position of Patterson (1977) as in conflict with the theory. Since it is Patterson's framework that is accepted here, Moss and Moss-Salentijn's claim must be addressed.

Moss and Moss-Salentijn (1983: 6) describe a tissue intermediate between notochordal and true cartilaginous tissue as *chondroid*. Chondroid tissue has large, vesicular cells in sparse matrix and resembles young cartilage (Moss, 1961: 103). Chondroid is distinguished from cartilage since the tissue binds with mucicarmine and thionin but is unable to bind with methylene blue below a pH of 4.6. Moss (1961) shows that chondroid tissue is able to undergo its own form of direct osteogenesis, called chondroidal osteogenesis. 'Superficially there is a similarity between the chondroidal osteogenesis and the transformation of mammalian secondary cartilage into bone ... In both tissues there is a metaplasia of the original tissue into osteoblasts (osteocytes?), with a concomitant alteration in the surrounding matrix and ground substance ending in the calcification of these extracellular areas. The differential staining reactions of these two tissues ... probably allows us to claim a basic disparity exists between them' (Moss, 1961: 103). Moss and Moss-Salentijn claim that chondroidal osteogenesis also occurs 'during the healing of bone fractures in some fishes' (Moss and Moss-Salentijn, 1983: 11). However, let us look at the original report: 'Pritchard and Ruzicka (1950) compared the fracture reactions in frog, lizard and rat ... Our data abundantly confirm their report that in non-mammals an intermediate cartilage-like tissue type is frequently found in the callus, which is quite capable of direct modulation into bone tissue' (Moss, 1962: 54). The cartilage-like tissue formed only when cartilage bones were fractured. Specifically, the jaws were examined (Moss, 1962: 55). Moss and Moss-Salentijn (1983) make no attempt to justify his equation of this callus cartilage-like tissue with chondroid. It seems enough to state that they are 'cartilage-like.'

Moss and Moss-Salentijn (1983) have equated different classes of tissue and different processes of differentiation according to their particular purposes. If they wish to demonstrate that fishes, as 'lower' vertebrates, have a tissue intermediate between those distinguishable in mammals, then chondroid is recognised as a (somewhat) distinct class of tissue. However, if Moss and Moss-Salentijn wish to emphasise the widespread occurrence of secondary cartilage in vertebrates, chondroid is subsumed within that class. In most cases the justification for the equation of classes of tissue is lacking, and may even be contradicted when the original reports are examined. All this seems to stem from Moss and Moss-Salentijn's advocation of the modulation theory of the vertebrate skeleton, so it would seem right to deny the implications of the theory and follow Patterson (1977).

Chapter 6.2: Chondroid Bone and Secondary Cartilage

There is some confusion over the terms 'chondroid' and 'chondroidal osteogenesis'. Moss (1961) uses chondroid to refer to what Beresford (1993) calls Type I chondroid bone. Type I chondroid bone consists of cartilage cells in a bone matrix, and in whole mounts has the histochemistry of bone (Haines, 1937; Weisel, 1967; Moss, 1961; Huysseune *et al.*, 1986; Taylor *et al.*, 1994). The tissue stains with alizarin red, but not with alcian blue. The report of Huysseune and Verraes (1990) lies somewhat at odds with the simple picture gained from whole mounts. They describe how chondroid bone reacts with alcian blue to a lesser extent than cartilage, but to a greater extent than bone, which can be made to stain at very low pH. Huysseune and Sire (1990) however remain confident of the bone-like properties of the chondroid bone matrix. Moss (1961) describes the process of chondroidal osteogenesis whereby chondroid bone is converted into true bone (Beresford, 1993; see also Schmid-Monnard, 1883; Haines, 1937; Weisel, 1967). The term 'chondroidal osteogenesis' would appear to be most appropriately used to describe this process.

Beresford (1993) refers to a number of chondroid tissues, which Benjamin (1989a, 1989b, 1990) nonetheless describes as cartilages. These tissues form a spectrum of types, of which mammalian cartilage is seen to be a specialised version. Benjamin describes two processes of 'chondroidal osteogenesis', one in which hyaline-cell cartilage is converted into true bone (in the dentary of *Garra taeniata*, Benjamin, 1989b: figure 3a) and a second in which cell-rich hyaline cartilage is converted into chondroid bone (in the anguloarticular of *Sphaerichthys osphromenoides*, Benjamin, 1990: figure 24). Neither is the process of chondroidal osteogenesis described by Moss (1961) and

as Benjamin tends towards describing 'chondroid' tissues as cartilage, it would seem appropriate to use a different term, such as secondary osteogenesis. Otherwise, we are in danger of confusing chondroid bone with secondary cartilage, as did Moss and Moss-Salentijn (1983).

It is interesting that cartilage cells can develop in the dermal skeleton of fishes. This phenomenon has previously been recorded in the dentary and anguloarticular of *Trigla capensis* (Haines, 1937: figure 16) and the parasphenoid of *Astatotilapia elegans* (Huysseune *et al.*, 1986: figures 1-3). The fact that the matrix composition of the two tissues is different should not be obscured. Beresford (1993) emphasises matrix composition in his classification of skeletal tissues. For example, he groups together dentine, bone and cementum on this basis. However, where calcified cartilage forms part of the skeleton of osteostracans, sharks, placoderms and acanthodians Beresford puzzlingly describes the tissue as chondroid bone type II. This tissue, being calcified rather than ossified, are mineralised with calcium carbonate not calcium phosphate.

Chapter 6.3: Secondary Cartilage in Teleosts

Benjamin (1989a) provides the first detailed report of secondary cartilage in a teleost, namely the black molly *Poecilia sphenops*. Hyaline-cell cartilage was found to be derived from the periosteal cells of the dentary and maxilla after intramembranous ossification, probably in response to jaw movements. Ossification of the dentary and maxilla commenced before birth (mollies are livebearers). Hyaline cells were first noticed 3½ weeks after birth. Hyaline-cell cartilage develops between the maxilla and the coronoid process of the dentary, uniting the two. The cartilage then separates off as a meniscus, remaining tenuously attached to the lateral aspect of the maxilla. In this case, hyaline-cell cartilage does not transform into bone. Benjamin describes hyaline-cell cartilage as mild staining, in comparison with the strongly staining *Zellknorpel* of the gill filaments (Benjamin, 1990: 154).

Hyaline-cell cartilage is found to merge gradually with bone when it is involved in secondary osteogenesis. Benjamin (1989b: 289) records this state of affairs on the hyomandibula of *Alestes longipinnis* and the dentary of *Garra taeniata* (see his figure 3a). The more familiar role for hyaline-cell cartilage is as the support for various otherwise soft structures, for example the lips, rostral folds, adhesive discs, barbels and nasal skin flaps. However, it would seem sensible to suggest that in *Garra taeniata* this cartilage plays a part in the development of dermal bones.

Moss (1969) states that dermal bone may ossify in several ways, including metaplasia of secondary cartilage (Moss, 1969: 514). He cites Moss (1961) but here, as we have seen, the chondroid tissue discussed is distinguished from cartilage by its staining reactions. Discussing the dermal sclerifications of reptiles, Moss concludes: 'We found no evidence for participation of any variety of cartilaginous tissues' (Moss, 1969: 517). Here he is saying that metaplasia of cartilage is a possible mode of bone formation in the reptilian dermal skeleton, but is not actually found. In a later report the possibility has become actuality: 'Reptilian dermal sclerifications exhibit quite a variety of histological types, and they may be compound in nature. When bone tissue is formed, it may be produced in at least three ways: periosteal osteogenesis, tendinous ossification, and metaplasia of secondary cartilage' (Moss, 1972: 33). However, no evidence is presented and the claim seems to be pure wishful thinking.

In a later section of their review article, Moss and Moss-Salentijn (1983) discuss the evidence for the presence of secondary cartilage in fishes, amphibians and reptiles: 'this often large-celled, minimally matrix containing cartilage is also normally found in the dermal skeleton of some reptiles (Moss, 1969, 1972) as well as at the joint surfaces of many bony fishes (Moss, 1961). A closely similar tissue is found in fracture sites of amphibians and reptiles (Pritchard and Ruzicka, 1950). During ontogeny secondary cartilage is replaced either by endochondral ossification or by direct transformation into bone (Moss, 1961, in fishes)' (Moss and Moss-Salentijn, 1983: 21). Four points arise from this passage:

1. The report of any variety of cartilage in the dermal skeleton of reptiles contradicts the original observations (Moss, 1969: 517).
2. In referring to the joint surfaces of bony fishes, Moss and Moss-Salentijn equate fish chondroid with mammalian secondary cartilage. This is justified on the basis of cellular histology, both comprise large cells in sparse matrix, but not on the basis of their staining reactions (Moss, 1961: 103). Chondroid has been treated as a distinct tissue earlier in the same review (Moss and Moss-Salentijn, 1983: 11).
3. Having equated chondroid tissue with the callus cartilage-like tissue in fishes, amphibians and reptiles (Moss and Moss-Salentijn, 1983: 11) they then equate both with mammalian secondary cartilage.
4. Moss and Moss-Salentijn equate chondroidal osteogenesis in fishes with metaplasia of secondary cartilage in mammals. Chondroidal osteogenesis was discussed earlier in the same review as a distinct process (Moss and Moss-Salentijn, 1983: 11) and 'a basic disparity' was held to exist between the two processes in the original report (Moss, 1961: 103).

Benjamin (1990: 169) draws attention to two descriptions of teleost secondary cartilage in the literature, namely Norman (1926) and Nigrelli and Gordon (1946). Norman describes the rostral cartilage in *Salmo* as derived from paired premaxillary cartilages (Norman, 1926: 441). The cartilage appear late in development, subsequent to the ossification of the premaxillae themselves. The posterior ends of the premaxillae are said to be embedded in the substance of the cartilage. Benjamin interprets this as a possible case of secondary cartilage. In macrourids the premaxillae sometimes grip the rostral cartilage closely. It may be that clearing and staining would reveal this to be the explanation in *Salmo*.

Nigrelli and Gordon (1946) describe a tumour extending from the opercular region to the lower jaw in an individual of the jewel cichlid *Hemichromis bimaculatus*. The tumour was an osteochondroma, the main constituent of which being a cell-rich cartilage. The bones involved were the preoperculum, operculum, suboperculum, interoperculum, branchiostegals, maxilla and infraorbitals. All these bones are dermal and except for the maxilla are found to stain with alcian blue in *Coryphaenoides* (see next section). Nigrelli and Gordon suggest that the cartilage developed (secondarily) from the periosteum of the dermal bones, perhaps after fracture of the operculum. To set against this interpretation though, Moss (1962) discovered no callus cartilage when the operculum in cichlids was fractured.

In rattails I have observed that alcian blue stains specific portions of the following dermal bones: nasal, frontal; first, second and third infraorbitals; preoperculum, operculum, suboperculum, interoperculum; branchiostegals. The pattern of staining is constant across well-stained specimens of a number of different species (see Figures 10A, 29B, 29C, 31, 32B, 33B, 33C; 38B). The cartilage would appear to persist late in development. In contrast to the situation in the black molly, cartilage is found at the margins of the bone, not at the joints.

There is evidence that the cartilage is involved in an ossification process. Such a process can be inferred from comparing a small specimen of *C. guentheri* and a larger specimen of *C. anguliceps* (Figure 31). These two species reach the same maximum length. In both specimens the posterior and ventral margins of the interoperculum stain with alcian blue. The region is more extensive in *C. guentheri*, whereas in *C. anguliceps* the bony region has encroached upon it. A series of 'ribs' extending from the bony region stain with alcian blue in *C. guentheri*, but with alizarin red in *C. anguliceps*. In all species, the preoperculum has a series of ribs extending from a central bony region into cartilage. In fact, a single rib can be traced as staining proximally with alizarin red, and distally with alcian blue (Figure 31B). The cartilage observed in *Coryphaenoides* is therefore

intimately associated with bone and forms an integral part of the dermal elements in which it is found. This is to be expected if the cartilage is being converted into bone.

The most obvious way to account for these observations is to suggest that the dermal bones in *Coryphaenoides* are preformed in cartilage, that is, they have become cartilage bones. For example, the conditions of the interoperculum in *Coryphaenoides guentheri* and *C. anguliceps* could be seen as successive stages in the replacement of a cartilaginous template by bone. The conversion of a dermal bone to a cartilage bone does not, however, occur even in birds and mammals: 'The dermal bones in many birds and mammals acquire areas of secondary or adventitious cartilage which may play an important part in subsequent growth, but the structure, development and response to various stimuli of this tissue all indicate that it is quite separate and distinct from the primary cartilage of the endoskeleton. Its occurrence can in no way be taken as an example of a dermal bone being converted into a cartilage replacing bone' (Moore, 1981: 69). It is very important to understand this point. Lansdown (1968) described the clavicle of the Japanese quail, *Coturnix c. japonica*, as preformed in cartilage and undergoing rapid endochondral ossification. Andersen (1963) similarly did not regard the cartilages developing in the human clavicle as secondary. Hall (1986) has since shown that in the chick cartilage forms from the periosteum after intramembranous ossification has commenced. He has also established a link with embryonic motility, at a lower threshold than with the craniofacial bones. The most appropriate inference for *Coryphaenoides* is not that there is a cartilaginous precursor, but that secondary cartilage is added to the margin of the dermal bone, which is converted to bone as the element grows.

It would seem most obvious to assume that the cartilage tissue in the dermal skeleton of *Coryphaenoides* is hyaline-cell cartilage. However, this has to tested through further histological examination. Similarly the origin of the cartilage matrix, from the periosteal cells, has to be established. A question remains as to the stimulus for chondrogenesis, whether it is in fact a motility stimulus as has been the case for birds and mammals. It may be of some significance that the dermal bones in which secondary cartilage has been recorded in *Coryphaenoides* are associated either with the opercular and branchiostegal membranes, which are expandable, or with sensory canals.

Another intriguing question is the phylogenetic distribution of secondary cartilage. There is circumstantial evidence that secondary cartilage occurs in the opercular bones of paracanthopterygians and esociforms. The distribution of secondary cartilage in other teleosts

must be investigated. Benjamin (1989a) suggests that the capacity for secondary chondrogenesis evolved early in vertebrate history. However, it has not so far been detected in amphibians or reptiles (Hall and Hanken, 1985; Irwin and Ferguson, 1986), and we may have to entertain the suggestion that secondary chondrogenesis has evolved at least three times: in birds, mammals and teleosts. It is puzzle why secondary cartilage should have features in common in birds and mammals if it has evolved separately. What are the developmental or adaptational constraints involved? Benjamin (1989a) commends the suggestion that Murray's (1963) term 'adventitious cartilage' be used for the tightly defined case and secondary cartilage for the broader association of cartilage with the dermal skeleton: 'This would avoid our needing to know whether the periosteum is involved in the soft tissue development, and it would remove the need to establish the temporal sequence in which tissues appear' (Benjamin, 1989a: 153). It would be unfortunate, however, if interesting research questions were stifled by such a change in terminology.

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Data Matrix of Morphological Characters for Rattail Analysis

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Melanonus zugmayeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hymenocephalus italicus	0	1	1	0	0	1	1	0	0	0	1	1	0	0
Echinomacrurus mollis	0	1	0	0	0	?	1	0	0	?	1	?	0	0
Mataeocephalus microstomus	0	1	0	0	1	1	1	0	0	?	2	1	0	2
Cetonurus globiceps	?	?	?	0	1	0	1	0	0	0	1	0	0	0
Sphagemacrurus hirundo	0	1	0	0	1	1	1	0	0	0	1	1	0	0
Nezumia aequalis	0	1	0	0	1	1	1	0	0	0	1	1	0	0
Trachonurus villosus	0	1	0	1	1	1	1	0	0	0	1	0	0	0
Malacocephalus laevis	0	1	0	1	1	1	0	0	0	0	1	0	0	3
Ventrifossa sp.	0	1	0	1	1	1	0	0	0	0	1	0	0	0
Lionurus filicauda	0	1	?	3	0	0	1	0	1	1	0	0	1	?
Lionurus carapinus	0	1	1	3	0	0	1	0	0	1	1	0	1	?
Chalinura leptolepis	0	0	0	3	0	0	1	1	1	1	0	0	1	?
Chalinura brevibarbis	0	0	?	3	0	0	1	0	1	1	1	0	1	?
Nematonurus armatus	0	1	0	3	0	0	1	1	1	1	0	0	1	?
Nematonurus yaquinae	0	1	0	3	0	0	1	1	1	1	0	0	1	?
Coryphaenoides rupestris	1	1	1	2	0	1	1	0	0	0	1	1	0	1
Coryphaenoides guentheri	1	1	0	0	0	1	1	0	0	0	1	1	0	1
Coryphaenoides mexicanus	1	1	0	0	0	1	1	0	0	?	1	1	0	1
Coryphaenoides anguliceps	1	1	0	2	0	1	1	0	0	0	1	0	0	1
Coryphaenoides zaniophorus	1	1	0	2	0	1	1	1	1	0	0	0	0	1
Caelorinchus caelorhincus	1	1	0	2	0	1	1	1	1	0	1	1	0	2
Macrourus berglax	1	1	0	2	1	1	1	1	1	0	1	0	0	2

Table 1

Data Matrix of Morphological Characters for Rattail Analysis

	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Melanonus zugmayeri	?	0	0	0	0	0	0	0	?	0	0	?	0	0
Hymenocephalus italicus	?	0	1	0	0	1	0	0	0	0	1	0	0	0
Echinomacrurus mollis	?	0	1	2	0	1	0	0	0	1	1	0	1	0
Mataeocephalus microstomus	?	1	1	5	1	0	0	0	0	1	1	1	1	0
Cetonurus globiceps	?	0	1	2	0	1	0	0	0	0	?	?	1	0
Sphagemacrurus hirundo	?	0	1	0	0	1	0	0	0	0	1	0	1	0
Nezumia aequalis	?	0	1	0	0	1	0	0	0	0	0	?	1	0
Trachonurus villosus	?	0	1	0	0	1	0	0	0	0	1	1	0	0
Malacocephalus laevis	?	1	1	0	0	1	0	0	0	0	1	1	1	0
Ventrifossa sp.	?	0	0	0	0	1	0	0	0	0	1	1	1	0
Lionurus filicauda	0	0	1	0	0	1	0	1	0	0	1	1	0	1
Lionurus carapinus	0	0	1	0	0	1	0	1	0	0	1	0	0	1
Chalinura leptolepis	1	0	1	0	0	1	0	1	0	1	1	1	1	0
Chalinura brevibarbis	1	0	0	0	0	1	0	1	0	1	1	1	1	0
Nematonurus armatus	0	0	1	0	0	1	0	1	0	1	1	1	1	0
Nematonurus yaquinae	0	0	0	0	0	1	0	1	0	1	1	1	1	0
Coryphaenoides rupestris	?	0	1	0	0	1	0	1	0	0	1	0	1	0
Coryphaenoides guentheri	?	0	1	0	0	1	0	1	1	0	0	1	1	0
Coryphaenoides mexicanus	?	0	1	2	0	1	0	1	0	0	0	1	1	0
Coryphaenoides anguliceps	?	0	1	1	0	1	0	1	0	0	1	0	1	0
Coryphaenoides zaniophorus	?	1	1	3	1	1	0	0	1	0	1	0	1	0
Caelorinchus caelorhincus	?	1	1	4	1	0	1	0	1	0	0	?	1	0
Macrourus berglax	?	1	1	4	1	0	1	0	1	0	0	?	1	0

Table 1

Data Matrix of Morphological Characters for Rattail Analysis

	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Melanonus zugmayeri	0	0	0	0	0	0	?	0	0	0	0	0	0	0
Hymenocephalus italicus	0	1	0	0	0	0	?	0	0	0	0	0	0	0
Echinomacrurus mollis	0	0	1	?	0	0	?	0	0	0	0	0	0	0
Mataeocephalus microstomus	0	1	0	1	0	0	?	0	1	1	0	1	0	1
Cetonurus globiceps	0	1	0	0	0	0	?	0	0	0	0	0	0	0
Sphagemacrurus hirundo	0	1	1	?	0	0	?	0	0	0	0	0	0	0
Nezumia aequalis	0	1	0	1	0	0	?	0	1	0	0	0	0	1
Trachonurus villosus	0	1	0	1	0	0	?	1	0	0	0	0	0	1
Malacocephalus laevis	1	1	0	1	0	1	0	0	0	0	0	1	0	1
Ventrifossa sp.	1	1	0	1	0	1	0	0	0	0	0	0	0	0
Lionurus filicauda	0	0	1	?	0	1	0	0	0	0	1	0	0	0
Lionurus carapinus	0	0	1	?	1	1	0	0	0	0	1	0	0	0
Chalinura leptolepis	0	0	1	?	0	1	0	1	0	0	1	0	0	0
Chalinura brevibarbis	0	0	1	?	0	1	0	0	0	0	1	1	0	0
Nematonurus armatus	0	0	1	?	0	1	0	1	0	0	1	1	0	0
Nematonurus yaquinae	0	0	1	?	0	1	0	1	0	0	1	0	0	0
Coryphaenoides rupestris	0	1	0	0	0	1	1	0	0	0	0	1	0	0
Coryphaenoides guentheri	0	1	0	0	0	1	1	0	0	0	0	1	0	0
Coryphaenoides mexicanus	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Coryphaenoides anguliceps	0	0	1	?	0	1	1	0	0	0	1	0	0	0
Coryphaenoides zaniophorus	0	0	0	0	0	1	1	0	0	0	0	1	1	0
Caelorinchus caelorhincus	0	0	0	0	0	1	0	0	0	1	0	0	1	0
Macrourus berglax	0	0	0	0	1	1	0	0	0	1	0	1	1	0

Table 1

Data Matrix of Morphological Characters for Rattail Analysis

	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Melanonus zugmayeri	0	0	0	0	0	0	0	0	0	0	0	0	?	0
Hymenocephalus italicus	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Echinomacrurus mollis	0	0	0	0	0	0	0	1	0	?	1	0	0	1
Mataeocephalus microstomus	0	0	1	1	1	1	1	1	0	1	1	0	1	1
Cetonurus globiceps	0	?	0	1	0	0	0	1	0	1	1	0	1	1
Sphagemacrurus hirundo	0	0	0	1	0	0	0	1	0	1	1	0	0	1
Nezumia aequalis	0	0	0	1	0	0	0	0	1	1	1	0	1	1
Trachonurus villosus	0	1	0	1	0	0	0	1	0	1	0	0	1	1
Malacocephalus laevis	0	0	0	1	0	0	0	0	1	0	1	0	1	1
Ventrifossa sp.	0	0	0	1	0	0	0	0	1	0	1	0	1	1
Lionurus filicauda	2	1	1	1	1	1	0	0	1	1	1	1	1	1
Lionurus carapinus	2	0	1	1	1	1	0	0	1	1	1	1	1	1
Chalinura leptolepis	0	0	1	1	0	1	0	0	0	1	1	1	1	1
Chalinura brevibarbis	0	0	1	1	1	0	0	0	0	1	1	1	1	1
Nematonurus armatus	3	0	1	1	0	1	0	0	1	1	1	1	1	1
Nematonurus yaquinae	3	0	1	1	0	1	0	0	1	1	1	1	1	1
Coryphaenoides rupestris	0	1	0	1	0	0	0	0	1	0	0	1	1	1
Coryphaenoides guentheri	1	0	0	1	0	0	1	0	1	0	0	1	1	2
Coryphaenoides mexicanus	0	0	0	1	1	0	1	0	1	0	0	1	1	2
Coryphaenoides anguliceps	0	0	0	1	0	0	1	0	1	0	0	1	1	2
Coryphaenoides zaniophorus	1	1	1	1	1	0	1	0	1	0	0	1	1	2
Caelorinchus caelorhincus	1	0	1	1	1	1	1	1	1	1	0	1	1	2
Macrourus berglax	1	1	1	1	1	1	1	1	1	1	0	1	1	3

Table 1

Data Matrix of Morphological Characters for Rattail Analysis

	57	58	59	60	61	62	63	64	65	66	67	68	69	70
Melanonus zugmayeri	0	0	0	?	0	0	?	0	0	?	?	0	0	0
Hymenocephalus italicus	0	0	0	?	0	0	0	0	0	?	?	0	0	0
Echinomacrurus mollis	1	0	0	?	0	0	1	?	?	?	?	0	0	0
Mataeocephalus microstomus	1	0	1	0	0	0	1	0	0	?	?	1	?	0
Cetonurus globiceps	1	0	1	0	0	0	1	0	0	?	?	0	0	0
Sphagemacrurus hirundo	1	0	1	0	0	0	0	1	0	0	0	0	1	0
Nezumia aequalis	1	0	1	0	0	0	1	1	0	0	0	0	0	1
Trachonurus villosus	1	0	1	0	0	0	1	1	0	0	0	1	?	1
Malacocephalus laevis	0	1	1	1	0	0	1	1	0	0	0	1	?	1
Ventrifossa sp.	1	1	1	1	0	0	1	1	0	0	0	0	1	1
Lionurus filicauda	1	0	1	1	0	0	1	1	0	1	1	0	1	0
Lionurus carapinus	1	0	1	1	0	0	1	1	0	1	1	0	1	0
Chalinura leptolepis	1	0	1	1	0	0	1	1	0	1	0	0	1	0
Chalinura brevibarbis	1	0	1	1	0	0	1	1	0	1	0	0	1	0
Nematonurus armatus	1	0	1	1	0	0	1	1	0	1	0	0	1	0
Nematonurus yaquinae	1	0	1	1	0	0	1	1	0	1	0	0	1	0
Coryphaenoides rupestris	1	0	1	1	0	0	1	1	0	1	0	0	1	0
Coryphaenoides guentheri	1	0	0	?	0	0	0	0	0	?	?	1	?	0
Coryphaenoides mexicanus	1	0	0	?	0	0	1	1	0	1	0	1	?	0
Coryphaenoides anguliceps	1	0	0	?	0	0	1	1	0	1	0	1	?	0
Coryphaenoides zaniophorus	1	0	0	?	0	0	1	0	0	?	?	0	1	0
Caelorinchus caelorhincus	1	0	1	1	1	1	1	0	1	0	0	1	?	0
Macrourus berglax	1	0	1	1	1	1	1	0	1	0	0	1	?	0

Table 1

Data Matrix of Morphological Characters for Rattail Analysis

	71	72	73	74	75	76	77	78	79	80	81	82	83	84
Melanonus zugmayeri	0	0	0	?	1	0	0	?	0	0	0	0	0	0
Hymenocephalus italicus	0	0	1	0	0	0	2	0	0	1	0	0	0	0
Echinomacrurus mollis	1	0	1	0	0	0	0	?	1	1	0	0	0	1
Mataeocephalus microstomus	1	0	1	1	0	1	0	?	0	1	0	0	0	1
Cetonurus globiceps	0	0	1	1	0	0	2	1	1	0	1	0	0	1
Sphagemacrurus hirundo	0	0	1	1	0	0	2	1	0	1	0	0	0	1
Nezumia aequalis	1	1	1	1	0	0	2	1	0	1	0	0	0	0
Trachonurus villosus	1	0	1	0	0	0	2	1	0	0	0	0	0	1
Malacocephalus laevis	0	0	1	0	0	0	2	1	0	0	0	0	0	1
Ventrifossa sp.	0	0	1	1	0	0	2	1	0	0	0	0	0	0
Lionurus filicauda	1	0	0	1	2	0	0	?	0	1	1	1	0	1
Lionurus carapinus	1	0	0	1	2	0	0	?	0	1	1	1	0	1
Chalinura leptolepis	0	0	0	1	2	0	0	?	0	1	1	1	0	1
Chalinura brevibarbis	0	0	0	1	2	0	0	?	0	1	1	1	0	1
Nematonurus armatus	1	0	0	1	2	0	0	?	0	1	1	1	0	1
Nematonurus yaquinae	1	0	0	1	2	0	0	?	0	1	1	1	0	1
Coryphaenoides rupestris	1	1	1	1	1	0	0	?	1	0	0	0	0	1
Coryphaenoides guentheri	1	1	1	1	1	0	0	?	0	1	0	1	1	1
Coryphaenoides mexicanus	1	1	1	1	1	0	0	?	0	1	0	0	0	1
Coryphaenoides anguliceps	1	1	1	1	1	0	0	?	0	1	0	0	0	1
Coryphaenoides zaniophorus	1	1	1	1	1	0	0	?	0	1	0	0	1	1
Caelorinchus caelorhincus	1	1	1	0	1	1	2	0	0	1	1	1	0	1
Macrourus berglax	1	0	1	1	1	1	1	?	0	1	1	1	0	1

Table 1

Data Matrix of Morphological Characters for Rattail Analysis

	85	86
Melanonus zugmayeri	1	0
Hymenocephalus italicus	0	0
Echinomacrurus mollis	0	1
Mataeocephalus microstomus	0	1
Cetonurus globiceps	0	1
Sphagemacrurus hirundo	0	1
Nezumia aequalis	2	1
Trachonurus villosus	1	1
Malacocephalus laevis	0	1
Ventrifossa sp.	0	1
Lionurus filicauda	2	1
Lionurus carapinus	2	1
Chalinura leptolepis	2	1
Chalinura brevibarbis	2	1
Nematonurus armatus	2	1
Nematonurus yaquinae	2	1
Coryphaenoides rupestris	2	1
Coryphaenoides guentheri	2	1
Coryphaenoides mexicanus	2	1
Coryphaenoides anguliceps	2	1
Coryphaenoides zaniophorus	2	1
Caelorinchus caelorhincus	2	1
Macrourus berglax	1	1

Table 1

Data Matrix for WOGADS Analysis

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Percopsidae	0	0	0	?	0	0	0	0	0	0	0	0	1	0	0
Amblyopsidae	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0
Aphredoderidae	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0
Carapidae	2	0	0	?	1	0	1	0	0	0	0	0	0	0	0
Ophidiidae	2	0	0	?	?	0	1	0	0	0	0	0	0	0	0
Bythitoidei	2	0	0	?	?	0	1	0	0	0	0	0	0	0	0
Lophiiformes	2	0	0	?	0	0	0	0	?	0	0	0	0	2	?
Batrachoidiformes	2	0	1	0	0	0	0	0	0	0	0	0	0	2	?
Melanonidae	0	0	0	?	0	0	0	0	0	0	0	1	0	0	0
Trachyrincidae	1	0	0	?	0	0	1	0	0	0	0	0	1	0	0
Macrouroididae	1	0	1	1	0	0	1	0	0	0	0	0	1	0	0
Macrouridae	1	0	1	?	0	1	1	0	0	0	0	0	1	0	0
Euclichthyidae	0	0	1	0	0	1	1	0	0	1	0	0	1	0	0
Bathygadidae	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0
Moridae	0	0	1	1	0	0	1	0	0	1	0	1	?	0	0
Steindachneriidae	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0
Macruronidae	0	0	1	0	0	0	?	0	0	1	0	1	0	0	1
Merlucciidae	0	0	1	0	0	0	0	1	1	1	1	2	0	1	1
Bregmacerotidae	0	0	0	?	0	0	0	0	0	1	1	2	0	0	0
Muraenolepididae	0	1	1	1	0	0	1	0	1	1	1	2	1	1	0
Gaidropsaridae	0	?	0	?	0	0	0	1	1	1	1	3	0	0	0
Phycidae	0	1	0	?	0	0	0	1	1	1	1	3	0	0	0
Ranicipitidae	0	0	0	?	0	0	0	0	1	1	1	3	0	0	0
Lotidae	0	0	0	?	1	0	0	1	1	1	1	3	0	0	1
Gadidae	0	?	0	?	0	0	0	0	1	1	1	3	0	1	0

Table 2

Data Matrix for WOGADS Analysis

	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Percopsidae	0	0	?	0	0	0	0	0	0	0	0	0	0	1	0
Amblyopsidae	1	0	?	0	0	0	0	0	0	0	1	?	0	0	0
Aphredoderidae	0	0	?	0	0	0	0	0	0	0	1	?	0	0	0
Carapidae	1	0	?	0	0	0	0	1	0	0	0	1	0	0	0
Ophidiidae	1	0	?	0	0	0	0	1	0	0	0	1	0	0	0
Bythitoidei	1	?	?	0	0	0	0	1	0	0	0	1	0	0	0
Lophiiformes	1	0	?	0	0	1	0	0	1	3	0	1	1	0	1
Batrachoidiformes	1	0	?	0	0	1	0	0	1	2	0	1	1	0	1
Melanonidae	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Trachyrincidae	1	1	0	0	0	0	0	0	0	1	0	1	0	1	0
Macrouroididae	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Macrouridae	1	1	0	0	0	0	0	?	0	0	0	1	0	1	0
Euclichthyidae	1	1	0	0	0	0	0	0	0	1	0	1	0	1	0
Bathygadidae	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Moridae	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Steindachneriidae	1	1	2	0	0	0	0	0	0	0	0	1	0	1	0
Macruronidae	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0
Merlucciidae	1	1	2	1	1	0	0	0	0	1	0	1	0	1	0
Bregmacerotidae	1	1	2	0	0	0	2	0	0	0	0	1	0	1	1
Muraenolepididae	1	1	2	0	0	0	1	0	0	0	0	1	0	1	0
Gaidropsaridae	1	1	2	0	0	0	1	0	0	0	0	1	0	1	0
Phycidae	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0
Ranicipitidae	1	1	1	0	0	0	1	0	0	0	0	1	0	1	0
Lotidae	1	1	2	0	0	0	1	0	0	1	0	1	0	1	0
Gadidae	1	1	2	1	0	0	0	0	0	0	0	1	0	1	0

Table 2

Data Matrix for WOGADS Analysis

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Percopsidae	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Amblyopsidae	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Aphredoderidae	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Carapidae	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0
Ophidiidae	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0
Bythitoidei	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0
Lophiiformes	?	0	0	0	0	?	?	0	?	0	0	0	0	0	0
Batrachoidiformes	?	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Melanonidae	0	0	0	0	0	1	1	0	?	1	1	0	0	1	2
Trachyrincidae	0	0	0	0	0	0	1	0	?	0	2	2	0	0	1
Macrouroididae	0	0	0	0	0	0	0	0	?	1	2	2	0	0	1
Macrouridae	0	0	0	0	0	0	1	0	?	1	2	?	0	0	1
Euclichthyidae	0	0	0	0	0	0	1	0	?	0	0	1	0	1	1
Bathygadidae	0	0	0	0	0	0	1	0	?	?	2	0	0	1	3
Moridae	0	0	0	0	?	1	1	0	?	0	2	0	0	1	1
Steindachneriidae	0	0	0	0	0	0	1	0	?	1	1	1	0	2	1
Macruronidae	0	0	0	0	1	0	2	0	?	0	0	?	0	2	4
Merlucciidae	1	1	0	1	1	1	2	1	1	0	0	0	0	2	4
Bregmacerotidae	?	2	0	0	?	1	1	1	0	0	2	2	0	0	1
Muraenolepididae	0	1	1	1	2	1	1	0	?	0	2	2	0	0	2
Gaidropsaridae	0	1	0	1	2	1	1	1	0	0	0	0	0	2	0
Phycidae	0	1	0	1	2	1	1	1	0	0	0	0	0	2	0
Ranicipitidae	0	1	0	1	0	1	1	1	0	0	0	0	0	2	0
Lotidae	0	1	1	1	0	1	2	1	1	0	0	0	0	2	0
Gadidae	1	1	1	1	2	1	2	1	1	0	0	0	0	2	0

Table 2

Data Matrix for WOGADS Analysis

	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Percopsidae	0	0	0	0	0	0	1	0	1	0	0	0	?	1	0
Amblyopsidae	0	0	0	0	0	0	0	0	1	0	0	0	?	1	0
Aphredoderidae	0	0	0	0	0	0	0	0	1	0	0	0	?	1	0
Carapidae	0	0	0	?	0	0	1	0	0	1	2	1	?	1	1
Ophidiidae	0	0	0	?	0	0	1	0	0	1	2	1	?	1	0
Bythitoidei	0	0	0	?	1	0	1	0	2	1	0	1	0	1	0
Lophiiformes	0	0	0	0	0	0	1	?	0	?	0	0	?	1	1
Batrachoidiformes	0	0	0	0	0	0	1	1	0	0	0	0	?	0	?
Melanonidae	1	2	0	1	1	0	0	0	0	0	2	0	?	0	1
Trachyrincidae	2	0	0	1	1	0	0	1	0	1	0	1	0	1	1
Macrouroididae	?	2	0	1	0	0	0	1	0	1	1	0	?	0	1
Macrouridae	3	2	0	1	0	0	0	0	?	0	0	1	0	1	1
Euclichthyidae	2	1	0	0	1	0	0	?	0	0	1	0	?	0	0
Bathygadidae	3	2	0	0	1	0	0	0	0	0	1	0	?	0	1
Moridae	3	2	1	0	1	0	0	0	0	0	1	0	?	0	1
Steindachneriidae	1	2	1	1	1	0	0	0	0	0	1	0	?	0	0
Macruronidae	1	2	?	1	1	0	0	0	0	0	1	0	?	0	1
Merlucciidae	1	2	0	1	1	0	0	1	0	0	?	?	?	0	1
Bregmacerotidae	2	2	1	1	1	0	0	?	0	0	0	1	0	1	1
Muraenolepididae	0	0	0	1	1	0	0	1	0	0	0	1	1	1	1
Gaidropsaridae	0	0	0	1	1	0	0	1	0	0	0	1	1	0	1
Phycidae	0	0	0	1	1	1	0	1	0	0	0	1	1	0	1
Ranicipitidae	0	2	0	1	1	0	0	1	0	0	0	0	?	0	1
Lotidae	0	0	0	1	1	1	0	1	0	2	0	1	1	0	1
Gadidae	0	0	0	1	1	0	0	1	0	2	0	1	1	0	1

Table 2

Data Matrix for WOGADS Analysis

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Percopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
Amblyopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
Aphredoderidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
Carapidae	?	0	0	0	0	0	0	1	0	0	0	0	0	1	?
Ophidiidae	0	0	1	0	0	0	0	?	?	?	0	0	0	1	?
Bythitoidei	1	0	0	0	0	0	0	1	?	?	0	0	1	1	?
Lophiiformes	?	1	1	0	0	0	0	0	0	0	0	0	1	0	?
Batrachoidiformes	2	1	0	0	0	0	0	0	0	0	0	0	1	0	?
Melanonidae	2	1	0	2	1	0	0	0	0	0	1	1	1	2	3
Trachyrincidae	2	1	0	1	2	0	1	3	0	1	1	0	0	0	?
Macrouroididae	1	1	0	0	0	0	0	0	0	1	1	0	0	2	2
Macrouridae	?	1	0	0	0	0	?	?	?	?	1	0	0	2	2
Euclichthyidae	1	1	0	0	0	0	2	2	0	0	1	0	0	2	3
Bathygadidae	0	1	0	2	0	0	2	2	1	?	1	0	0	2	2
Moridae	1	1	0	2	1	0	2	2	1	?	1	0	0	2	3
Steindachneriidae	0	1	0	2	1	2	2	2	0	0	1	1	1	2	2
Macruronidae	0	1	0	2	1	?	2	4	1	?	1	1	1	2	1
Merlucciidae	1	1	0	2	1	2	2	4	1	?	0	1	1	2	2
Bregmacerotidae	?	1	0	2	2	0	2	2	0	0	1	0	?	0	?
Muraenolepididae	1	1	0	1	0	1	1	1	0	0	2	0	0	2	2
Gaidropsaridae	1	1	0	1	0	0	2	2	0	0	0	0	1	0	?
Phycidae	1	1	0	1	0	1	0	1	0	0	0	0	1	0	?
Ranicipitidae	2	1	0	1	0	1	0	1	0	0	0	0	1	0	?
Lotidae	1	1	0	1	0	2	0	1	0	0	0	0	1	2	1
Gadidae	1	1	0	1	1	0	2	2	0	0	0	0	1	2	1

Table 2

Data Matrix for WOGADS Analysis

	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Percopsidae	?	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Amblyopsidae	?	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Aphredoderidae	?	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Carapidae	?	1	0	0	1	1	?	1	0	1	1	1	1	0	0
Ophidiidae	?	1	0	0	1	1	0	1	0	1	1	1	0	0	0
Bythitoidei	?	1	0	0	1	1	0	0	?	2	1	1	?	0	0
Lophiiformes	?	0	1	0	1	1	1	?	1	0	1	0	?	1	0
Batrachoidiformes	?	0	1	0	1	1	1	?	0	0	1	1	1	1	0
Melanonidae	1	1	1	0	1	2	0	1	1	0	?	0	0	0	0
Trachyrincidae	?	1	1	0	1	2	0	0	1	0	?	0	0	0	1
Macrouroididae	0	1	1	0	1	2	0	0	1	?	1	0	0	0	1
Macrouridae	1	1	1	0	1	2	0	0	1	0	?	0	0	0	?
Euclichthyidae	1	1	1	1	1	3	0	0	1	0	1	0	0	0	0
Bathygadidae	1	1	1	0	1	2	0	0	1	0	0	0	0	0	2
Moridae	1	1	1	0	1	1	0	0	1	2	?	0	0	0	0
Steindachneriidae	1	1	1	0	1	2	0	1	1	2	0	0	0	0	0
Macruronidae	1	1	1	0	1	?	0	1	1	2	0	0	0	0	0
Merlucciidae	1	1	1	0	1	3	0	1	1	2	0	0	0	0	0
Bregmacerotidae	?	1	1	0	1	0	0	0	1	0	?	0	0	0	0
Muraenolepididae	1	1	1	0	1	1	0	0	1	0	1	0	0	0	1
Gaidropsaridae	?	1	1	?	1	1	0	1	1	0	?	0	0	0	0
Phycidae	?	1	1	1	1	1	0	0	1	2	1	0	0	0	0
Ranicipitidae	?	1	1	1	1	3	0	1	1	2	1	0	0	0	0
Lotidae	1	1	1	0	1	4	0	1	1	2	?	0	0	0	0
Gadidae	0	1	1	0	1	2	0	0	1	2	?	0	0	0	0

Table 2

Data Matrix for WOGADS Analysis

	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
Percopsidae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Amblyopsidae	0	0	0	0	0	1	2	0	0	0	0	0	1	0	0
Aphredoderidae	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0
Carapidae	0	0	1	0	0	0	2	1	0	1	?	?	?	?	?
Ophidiidae	0	?	0	0	0	0	2	1	0	0	0	0	1	2	0
Bythitoidei	0	?	0	0	0	0	2	1	0	0	0	0	1	2	0
Lophiiformes	0	?	1	0	?	0	0	1	0	0	0	0	1	2	0
Batrachoidiformes	0	1	0	0	0	1	0	1	0	0	0	0	1	1	0
Melanonidae	0	0	0	0	0	0	2	1	0	0	0	1	0	1	1
Trachyrincidae	0	1	0	0	1	0	2	1	0	0	0	0	1	2	0
Macrouroididae	0	2	0	0	0	0	2	1	0	1	?	?	?	?	?
Macrouridae	0	2	0	0	1	0	0	3	0	1	?	?	?	?	?
Euclichthyidae	1	2	0	0	1	0	0	1	1	0	1	0	?	?	0
Bathygadidae	?	2	0	0	1	0	0	1	0	1	?	?	?	?	?
Moridae	1	2	0	0	1	0	0	2	?	0	1	0	0	1	0
Steindachneriidae	0	2	0	0	1	0	0	1	1	1	?	?	?	?	?
Macruronidae	1	2	0	0	?	0	?	1	?	0	0	0	1	2	0
Merlucciidae	1	2	0	0	1	0	1	2	0	0	1	0	1	1	1
Bregmacerotidae	1	4	1	1	1	0	2	2	1	0	1	0	1	1	0
Muraenolepididae	1	2	1	0	1	0	2	1	0	0	1	0	1	2	0
Gaidropsaridae	1	3	1	0	1	0	2	2	0	0	1	?	1	2	0
Phycidae	1	1	0	0	1	0	2	2	0	0	1	0	1	1	0
Ranicipitidae	1	1	0	0	1	0	2	2	0	0	1	0	0	2	0
Lotidae	?	2	0	?	?	0	2	2	0	0	0	1	1	2	1
Gadidae	1	1	0	1	1	0	2	2	0	0	0	1	1	2	1

Table 2

Data Matrix for WOGADS Analysis

	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Percopsidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Amblyopsidae	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Aphredoderidae	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0
Carapidae	?	0	0	1	1	1	0	0	0	0	0	0	2	0	0
Ophidiidae	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0
Bythitoidei	0	2	?	1	0	0	0	?	0	0	0	0	0	0	0
Lophiiformes	0	2	?	?	?	?	0	0	0	0	0	0	0	0	0
Batrachoidiformes	0	0	0	0	0	?	1	0	0	0	0	0	0	0	?
Melanonidae	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0
Trachyrincidae	0	2	1	1	0	1	1	0	0	1	0	1	0	0	0
Macrouroididae	?	2	?	1	0	1	1	0	0	1	0	1	0	?	0
Macrouridae	?	0	1	1	?	0	?	0	?	1	0	1	?	0	?
Euclichthyidae	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
Bathygadidae	?	0	1	1	?	0	?	0	1	0	0	0	0	0	0
Moridae	1	1	?	1	1	1	1	0	1	0	0	0	1	1	?
Steindachneriidae	?	0	1	1	1	0	0	1	0	0	0	0	1	1	1
Macruronidae	1	0	1	1	1	0	0	1	0	0	1	0	0	?	0
Merlucciidae	1	0	1	1	1	0	0	1	0	0	1	0	0	1	0
Bregmacerotidae	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Muraenolepididae	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Gaidropsaridae	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Phycidae	1	2	?	1	1	0	0	1	0	0	0	0	0	1	0
Ranicipitidae	1	0	1	1	1	?	0	0	0	0	0	0	0	0	0
Lotidae	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0
Gadidae	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0

Table 2

Data Matrix for WOGADS Analysis

	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Percopsidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Amblyopsidae	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Aphredoderidae	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0
Carapidae	?	0	0	1	1	1	0	0	0	0	0	0	2	0	0
Ophidiidae	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0
Bythitoidei	0	2	?	1	0	0	0	?	0	0	0	0	0	0	0
Lophiiformes	0	2	?	?	?	?	0	0	0	0	0	0	0	0	0
Batrachoidiformes	0	0	0	0	0	?	1	0	0	0	0	0	0	0	?
Melanonidae	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0
Trachyrincidae	0	2	1	1	0	1	1	0	0	1	0	1	0	0	0
Macrouroididae	?	2	?	1	0	1	1	0	0	1	0	1	0	?	0
Macrouridae	?	0	1	1	?	0	?	0	?	1	0	1	?	0	?
Euclichthyidae	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
Bathygadidae	?	0	1	1	?	0	?	0	1	0	0	0	0	0	0
Moridae	1	1	?	1	1	1	1	0	1	0	0	0	1	1	?
Steindachneriidae	?	0	1	1	1	0	0	1	0	0	0	0	1	1	1
Macruronidae	1	0	1	1	1	0	0	1	0	0	1	0	0	?	0
Merlucciidae	1	0	1	1	1	0	0	1	0	0	1	0	0	1	0
Bregmacerotidae	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Muraenolepididae	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Gaidropsaridae	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Phycidae	1	2	?	1	1	0	0	1	0	0	0	0	0	1	0
Ranicipitidae	1	0	1	1	1	?	0	0	0	0	0	0	0	0	0
Lotidae	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0
Gadidae	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0

Table 2

Data Matrix from Wilson, Siebenaller and Davis (1991)

	1	3	8	9	12	13	15	16	17	18	19	27	28	29
Albatrossia pectoralis	0	0	1	0	0	1	0	1	0	0	1	0	0	0
Chalinura leptolepis	0	0	0	1	1	0	0	0	1	1	1	1	1	0
Nematonurus armatus	0	0	1	1	1	0	0	0	0	0	0	0	0	0
Coryphaenoides rupestris	0	0	1	1	0	1	1	1	0	0	0	0	0	0
Coryphaenoides acrolepis	0	0	1	0	0	1	0	0	0	0	1	0	0	0
Coryphaenoides filifer	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Coryphaenoides mexicanus	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Coryphaenoides cinereus	0	0	0	0	0	1	1	0	0	0	1	0	1	1
Coryphaenoides zaniophorus	1	1	0	1	0	1	0	0	1	1	0	1	1	1
Caelorinchus occa	1	1	0	0	0	1	1	0	0	0	0	1	1	1

Table 3

Data Matrix from Wilson, Siebenaller and Davis (1991)

	31	34	36	37	38	39	40	41	42	43	44	45	46	48
Albatrossia pectoralis	1	1	1	1	1	0	1	1	1	0	0	1	1	1
Chalinura leptolepis	1	1	1	1	1	0	1	1	0	0	0	0	1	1
Nematonurus armatus	1	1	1	1	1	0	1	1	0	0	0	0	1	1
Coryphaenoides rupestris	0	1	1	0	0	0	1	1	0	1	0	1	0	0
Coryphaenoides acrolepis	0	0	1	0	1	0	1	1	1	1	0	1	1	1
Coryphaenoides filifer	0	1	1	0	1	0	1	1	1	1	1	1	1	1
Coryphaenoides mexicanus	0	1	0	0	0	1	0	0	0	0	0	1	1	1
Coryphaenoides cinereus	0	1	0	0	1	0	0	1	0	0	1	1	1	1
Coryphaenoides zaniophorus	1	1	1	0	0	1	1	0	0	0	1	1	1	1
Caelorinchus occa	0	0	0	1	1	0	1	0	0	0	1	1	0	0

Table 3

Data Matrix from Wilson, Siebenaller and Davis (1991)

	49	50	51	54	55	56
Albatrossia pectoralis	1	1	0	0	1	0
Chalinura leptolepis	1	1	0	0	0	1
Nematonurus armatus	1	1	0	0	0	1
Coryphaenoides rupestris	1	1	1	1	1	0
Coryphaenoides acrolepis	0	0	0	0	1	0
Coryphaenoides filifer	0	0	0	1	1	0
Coryphaenoides mexicanus	1	1	1	1	1	0
Coryphaenoides cinereus	0	0	0	1	1	0
Coryphaenoides zaniophorus	1	0	0	1	1	0
Caelorinchus occa	1	0	0	1	1	1

Table 3

Data Matrix of Morphological and Molecular Characters for Rattail Analysis

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Melanonus zugmayeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hymenocephalus italicus	0	1	1	0	0	1	1	0	0	0	1	1	0	0
Echinomacrurus mollis	0	1	0	0	0	?	1	0	0	?	1	?	0	0
Mataeocephalus microstomus	0	1	0	0	1	1	1	0	0	?	2	1	0	2
Cetonurus globiceps	?	?	?	0	1	0	1	0	0	0	1	0	0	0
Sphagemacrurus hirundo	0	1	0	0	1	1	1	0	0	0	1	1	0	0
Nezumia aequalis	0	1	0	0	1	1	1	0	0	0	1	1	0	0
Trachonurus villosus	0	1	0	1	1	1	1	0	0	0	1	0	0	0
Malacocephalus laevis	0	1	0	1	1	1	0	0	0	0	1	0	0	3
Ventrifossa sp.	0	1	0	1	1	1	0	0	0	0	1	0	0	0
Albatrossia pectoralis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lionurus filicauda	0	1	?	3	0	0	1	0	1	1	0	0	1	?
Lionurus carapinus	0	1	1	3	0	0	1	0	0	1	1	0	1	?
Chalinura leptolepis	0	0	0	3	0	0	1	1	1	1	0	0	1	?
Chalinura brevibarbis	0	0	?	3	0	0	1	0	1	1	1	0	1	?
Nematonurus armatus	0	1	0	3	0	0	1	1	1	1	0	0	1	?
Nematonurus yaquinae	0	1	0	3	0	0	1	1	1	1	0	0	1	?
Coryphaenoides rupestris	1	1	1	2	0	1	1	0	0	0	1	1	0	1
Coryphaenoides acrolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides filifer	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides guentheri	1	1	0	0	0	1	1	0	0	0	1	1	0	1
Coryphaenoides mexicanus	1	1	0	0	0	1	1	0	0	?	1	1	0	1
Coryphaenoides anguliceps	1	1	0	2	0	1	1	0	0	0	1	0	0	1
Coryphaenoides cinereus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides zaniophorus	1	1	0	2	0	1	1	1	1	0	0	0	0	1
Caelorinchus caelorhincus	1	1	0	2	0	1	1	1	1	0	1	1	0	2
Caelorinchus occa	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macrourus berglax	1	1	0	2	1	1	1	1	1	0	1	0	0	2

Table 4

Data Matrix of Morphological and Molecular Characters for Rattail Analysis

	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Melanonus zugmayeri	?	0	0	0	0	0	0	0	?	0	0	?	0	0
Hymenocephalus italicus	?	0	1	0	0	1	0	0	0	0	1	0	0	0
Echinomacrurus mollis	?	0	1	2	0	1	0	0	0	1	1	0	1	0
Mataeocephalus microstomus	?	1	1	5	1	0	0	0	0	1	1	1	1	0
Cetonurus globiceps	?	0	1	2	0	1	0	0	0	0	?	?	1	0
Sphagemacrurus hirundo	?	0	1	0	0	1	0	0	0	0	1	0	1	0
Nezumia aequalis	?	0	1	0	0	1	0	0	0	0	0	?	1	0
Trachonurus villosus	?	0	1	0	0	1	0	0	0	0	1	1	0	0
Malacocephalus laevis	?	1	1	0	0	1	0	0	0	0	1	1	1	0
Ventrifossa sp.	?	0	0	0	0	1	0	0	0	0	1	1	1	0
Albatrossia pectoralis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lionurus filicauda	0	0	1	0	0	1	0	1	0	0	1	1	0	1
Lionurus carapinus	0	0	1	0	0	1	0	1	0	0	1	0	0	1
Chalinura leptolepis	1	0	1	0	0	1	0	1	0	1	1	1	1	0
Chalinura brevibarbis	1	0	0	0	0	1	0	1	0	1	1	1	1	0
Nematonurus armatus	0	0	1	0	0	1	0	1	0	1	1	1	1	0
Nematonurus yaquinae	0	0	0	0	0	1	0	1	0	1	1	1	1	0
Coryphaenoides rupestris	?	0	1	0	0	1	0	1	0	0	1	0	1	0
Coryphaenoides acrolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides filifer	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides guentheri	?	0	1	0	0	1	0	1	1	0	0	1	1	0
Coryphaenoides mexicanus	?	0	1	2	0	1	0	1	0	0	0	1	1	0
Coryphaenoides anguliceps	?	0	1	1	0	1	0	1	0	0	1	0	1	0
Coryphaenoides cinereus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides zaniophorus	?	1	1	3	1	1	0	0	1	0	1	0	1	0
Caelorinchus caelorhincus	?	1	1	4	1	0	1	0	1	0	0	?	1	0
Caelorinchus occa	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macrourus berglax	?	1	1	4	1	0	1	0	1	0	0	?	1	0

Table 4

Data Matrix of Morphological and Molecular Characters for Rattail Analysis

	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Melanonus zugmayeri	0	0	0	0	0	0	?	0	0	0	0	0	0	0
Hymenocephalus italicus	0	1	0	0	0	0	?	0	0	0	0	0	0	0
Echinomacrurus mollis	0	0	1	?	0	0	?	0	0	0	0	0	0	0
Mataeocephalus microstomus	0	1	0	1	0	0	?	0	1	1	0	1	0	1
Cetonurus globiceps	0	1	0	0	0	0	?	0	0	0	0	0	0	0
Sphagemacrurus hirundo	0	1	1	?	0	0	?	0	0	0	0	0	0	0
Nezumia aequalis	0	1	0	1	0	0	?	0	1	0	0	0	0	1
Trachonurus villosus	0	1	0	1	0	0	?	1	0	0	0	0	0	1
Malacocephalus laevis	1	1	0	1	0	1	0	0	0	0	0	1	0	1
Ventrifossa sp.	1	1	0	1	0	1	0	0	0	0	0	0	0	0
Albatrossia pectoralis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lionurus filicauda	0	0	1	?	0	1	0	0	0	0	1	0	0	0
Lionurus carapinus	0	0	1	?	1	1	0	0	0	0	1	0	0	0
Chalinura leptolepis	0	0	1	?	0	1	0	1	0	0	1	0	0	0
Chalinura brevibarbis	0	0	1	?	0	1	0	0	0	0	1	1	0	0
Nematonurus armatus	0	0	1	?	0	1	0	1	0	0	1	1	0	0
Nematonurus yaquinae	0	0	1	?	0	1	0	1	0	0	1	0	0	0
Coryphaenoides rupestris	0	1	0	0	0	1	1	0	0	0	0	1	0	0
Coryphaenoides acrolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides filifer	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides guentheri	0	1	0	0	0	1	1	0	0	0	0	1	0	0
Coryphaenoides mexicanus	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Coryphaenoides anguliceps	0	0	1	?	0	1	1	0	0	0	1	0	0	0
Coryphaenoides cinereus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides zaniophorus	0	0	0	0	0	1	1	0	0	0	0	1	1	0
Caelorinchus caelorhincus	0	0	0	0	0	1	0	0	0	1	0	0	1	0
Caelorinchus occa	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macrourus berglax	0	0	0	0	1	1	0	0	0	1	0	1	1	0

Table 4

Data Matrix of Morphological and Molecular Characters for Rattail Analysis

	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Melanonus zugmayeri	0	0	0	0	0	0	0	0	0	0	0	0	?	0
Hymenocephalus italicus	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Echinomacrurus mollis	0	0	0	0	0	0	0	1	0	?	1	0	0	1
Mataeocephalus microstomus	0	0	1	1	1	1	1	1	0	1	1	0	1	1
Cetonurus globiceps	0	?	0	1	0	0	0	1	0	1	1	0	1	1
Sphagemacrurus hirundo	0	0	0	1	0	0	0	1	0	1	1	0	0	1
Nezumia aequalis	0	0	0	1	0	0	0	0	1	1	1	0	1	1
Trachonurus villosus	0	1	0	1	0	0	0	1	0	1	0	0	1	1
Malacocephalus laevis	0	0	0	1	0	0	0	0	1	0	1	0	1	1
Ventrifossa sp.	0	0	0	1	0	0	0	0	1	0	1	0	1	1
Albatrossia pectoralis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lionurus filicauda	2	1	1	1	1	1	0	0	1	1	1	1	1	1
Lionurus carapinus	2	0	1	1	1	1	0	0	1	1	1	1	1	1
Chalinura leptolepis	0	0	1	1	0	1	0	0	0	1	1	1	1	1
Chalinura brevibarbis	0	0	1	1	1	0	0	0	0	1	1	1	1	1
Nematonurus armatus	3	0	1	1	0	1	0	0	1	1	1	1	1	1
Nematonurus yaquinae	3	0	1	1	0	1	0	0	1	1	1	1	1	1
Coryphaenoides rupestris	0	1	0	1	0	0	0	0	1	0	0	1	1	1
Coryphaenoides acrolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides filifer	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides guentheri	1	0	0	1	0	0	1	0	1	0	0	1	1	2
Coryphaenoides mexicanus	0	0	0	1	1	0	1	0	1	0	0	1	1	2
Coryphaenoides anguliceps	0	0	0	1	0	0	1	0	1	0	0	1	1	2
Coryphaenoides cinereus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides zaniophorus	1	1	1	1	1	0	1	0	1	0	0	1	1	2
Caelorinchus caelorhincus	1	0	1	1	1	1	1	1	1	1	0	1	1	2
Caelorinchus occa	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macrourus berglax	1	1	1	1	1	1	1	1	1	1	0	1	1	3

Table 4

Data Matrix of Morphological and Molecular Characters for Rattail Analysis

	57	58	59	60	61	62	63	64	65	66	67	68	69	70
Melanonus zugmayeri	0	0	0	?	0	0	?	0	0	?	?	0	0	0
Hymenocephalus italicus	0	0	0	?	0	0	0	0	0	?	?	0	0	0
Echinomacrurus mollis	1	0	0	?	0	0	1	?	?	?	?	0	0	0
Mataeocephalus microstomus	1	0	1	0	0	0	1	0	0	?	?	1	?	0
Cetonurus globiceps	1	0	1	0	0	0	1	0	0	?	?	0	0	0
Sphagemacrurus hirundo	1	0	1	0	0	0	0	1	0	0	0	0	1	0
Nezumia aequalis	1	0	1	0	0	0	1	1	0	0	0	0	0	1
Trachonurus villosus	1	0	1	0	0	0	1	1	0	0	0	1	?	1
Malacocephalus laevis	0	1	1	1	0	0	1	1	0	0	0	1	?	1
Ventrifossa sp.	1	1	1	1	0	0	1	1	0	0	0	0	1	1
Albatrossia pectoralis	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Lionurus filicauda	1	0	1	1	0	0	1	1	0	1	1	0	1	0
Lionurus carapinus	1	0	1	1	0	0	1	1	0	1	1	0	1	0
Chalinura leptolepis	1	0	1	1	0	0	1	1	0	1	0	0	1	0
Chalinura brevibarbis	1	0	1	1	0	0	1	1	0	1	0	0	1	0
Nematonurus armatus	1	0	1	1	0	0	1	1	0	1	0	0	1	0
Nematonurus yaquinae	1	0	1	1	0	0	1	1	0	1	0	0	1	0
Coryphaenoides rupestris	1	0	1	1	0	0	1	1	0	1	0	0	1	0
Coryphaenoides acrolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Coryphaenoides filifer	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Coryphaenoides guentheri	1	0	0	?	0	0	0	0	0	?	?	1	?	0
Coryphaenoides mexicanus	1	0	0	?	0	0	1	1	0	1	0	1	?	0
Coryphaenoides anguliceps	1	0	0	?	0	0	1	1	0	1	0	1	?	0
Coryphaenoides cinereus	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Coryphaenoides zaniophorus	1	0	0	?	0	0	1	0	0	?	?	0	1	0
Caelorinchus caelorhincus	1	0	1	1	1	1	1	0	1	0	0	1	?	0
Caelorinchus occa	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Macrourus berglax	1	0	1	1	1	1	1	0	1	0	0	1	?	0

Table 4

Data Matrix of Morphological and Molecular Characters for Rattail Analysis

	71	72	73	74	75	76	77	78	79	80	81	82	83	84
Melanonus zugmayeri	0	0	0	?	1	0	0	?	0	0	0	0	0	0
Hymenocephalus italicus	0	0	1	0	0	0	2	0	0	1	0	0	0	0
Echinomacrurus mollis	1	0	1	0	0	0	0	?	1	1	0	0	0	1
Mataeocephalus microstomus	1	0	1	1	0	1	0	?	0	1	0	0	0	1
Cetonurus globiceps	0	0	1	1	0	0	2	1	1	0	1	0	0	1
Sphagemacrurus hirundo	0	0	1	1	0	0	2	1	0	1	0	0	0	1
Nezumia aequalis	1	1	1	1	0	0	2	1	0	1	0	0	0	0
Trachonurus villosus	1	0	1	0	0	0	2	1	0	0	0	0	0	1
Malacocephalus laevis	0	0	1	0	0	0	2	1	0	0	0	0	0	1
Ventrifossa sp.	0	0	1	1	0	0	2	1	0	0	0	0	0	0
Albatrossia pectoralis	1	0	1	1	0	0	0	?	0	1	0	0	0	1
Lionurus filicauda	1	0	0	1	2	0	0	?	0	1	1	1	0	1
Lionurus carapinus	1	0	0	1	2	0	0	?	0	1	1	1	0	1
Chalinura leptolepis	0	0	0	1	2	0	0	?	0	1	1	1	0	1
Chalinura brevibarbis	0	0	0	1	2	0	0	?	0	1	1	1	0	1
Nematonurus armatus	1	0	0	1	2	0	0	?	0	1	1	1	0	1
Nematonurus yaquinae	1	0	0	1	2	0	0	?	0	1	1	1	0	1
Coryphaenoides rupestris	1	1	1	1	1	0	0	?	1	0	0	0	0	1
Coryphaenoides acrolepis	1	1	1	1	1	0	0	?	0	1	0	0	0	1
Coryphaenoides filifer	1	1	1	1	1	0	0	?	0	1	0	0	0	1
Coryphaenoides guentheri	1	1	1	1	1	0	0	?	0	1	0	1	1	1
Coryphaenoides mexicanus	1	1	1	1	1	0	0	?	0	1	0	0	0	1
Coryphaenoides anguliceps	1	1	1	1	1	0	0	?	0	1	0	0	0	1
Coryphaenoides cinereus	1	1	1	1	1	0	0	?	0	1	0	0	0	1
Coryphaenoides zaniophorus	1	1	1	1	1	0	0	?	0	1	0	0	1	1
Caelorinchus caelorhincus	1	1	1	0	1	1	2	0	0	1	1	1	0	1
Caelorinchus occa	1	1	1	0	1	1	2	?	0	1	0	1	0	1
Macrourus berglax	1	0	1	1	1	1	1	?	0	1	1	1	0	1

Table 4

Data Matrix of Morphological and Molecular Characters for Rattail Analysis

	85	86	87	88	89	90	91	92	93	94	95	96	97	98
Melanonus zugmayeri	1	0	?	?	?	?	?	?	?	?	?	?	?	?
Hymenocephalus italicus	0	0	?	?	?	?	?	?	?	?	?	?	?	?
Echinomacrurus mollis	0	1	?	?	?	?	?	?	?	?	?	?	?	?
Mataeocephalus microstomus	0	1	?	?	?	?	?	?	?	?	?	?	?	?
Cetonurus globiceps	0	1	?	?	?	?	?	?	?	?	?	?	?	?
Sphagemacrurus hirundo	0	1	?	?	?	?	?	?	?	?	?	?	?	?
Nezumia aequalis	2	1	?	?	?	?	?	?	?	?	?	?	?	?
Trachonurus villosus	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Malacocephalus laevis	0	1	?	?	?	?	?	?	?	?	?	?	?	?
Ventrifossa sp.	0	1	?	?	?	?	?	?	?	?	?	?	?	?
Albatrossia pectoralis	2	1	0	0	1	0	0	1	0	1	0	0	1	0
Lionurus filicauda	2	1	?	?	?	?	?	?	?	?	?	?	?	?
Lionurus carapinus	2	1	?	?	?	?	?	?	?	?	?	?	?	?
Chalinura leptolepis	2	1	0	0	0	1	1	0	0	0	1	1	1	1
Chalinura brevibarbis	2	1	?	?	?	?	?	?	?	?	?	?	?	?
Nematonurus armatus	2	1	0	0	1	1	1	0	0	0	0	0	0	0
Nematonurus yaquinae	2	1	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides rupestris	2	1	0	0	1	1	0	1	1	1	0	0	0	0
Coryphaenoides acrolepis	2	1	0	0	1	0	0	1	0	0	0	0	1	0
Coryphaenoides filifer	2	1	0	0	1	0	0	1	0	0	0	0	0	0
Coryphaenoides guentheri	2	1	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides mexicanus	2	1	0	0	0	0	0	1	0	0	0	0	0	0
Coryphaenoides anguliceps	2	1	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides cinereus	2	1	0	0	0	0	0	1	1	0	0	0	1	0
Coryphaenoides zaniophorus	2	1	1	1	0	1	0	1	0	0	1	1	0	1
Caelorinchus caelorhincus	2	1	?	?	?	?	?	?	?	?	?	?	?	?
Caelorinchus occa	2	1	1	1	0	0	0	1	1	0	0	0	0	1
Macrourus berglax	1	1	?	?	?	?	?	?	?	?	?	?	?	?

Table 4

Data Matrix of Morphological and Molecular Characters for Rattail Analysis

	99	100	101	102	103	104	105	106	107	108	109	110	111	112
Melanonus zugmayeri	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hymenocephalus italicus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Echinomacrurus mollis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mataeocephalus microstomus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cetonurus globiceps	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sphagemacrurus hirundo	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nezumia aequalis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trachonurus villosus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Malacocephalus laevis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ventrifossa sp.	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Albatrossia pectoralis	0	0	1	1	1	1	1	0	1	1	1	0	0	1
Lionurus filicauda	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lionurus carapinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chalinura leptolepis	1	0	1	1	1	1	1	0	1	1	0	0	0	0
Chalinura brevibarbis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nematonurus armatus	0	0	1	1	1	1	1	0	1	1	0	0	0	0
Nematonurus yaquinae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides rupestris	0	0	0	1	1	0	0	0	1	1	0	1	0	1
Coryphaenoides acrolepis	0	0	0	0	1	0	1	0	1	1	1	1	0	1
Coryphaenoides filifer	0	0	0	1	1	0	1	0	1	1	1	1	1	1
Coryphaenoides guentheri	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides mexicanus	0	0	0	1	0	0	0	1	0	0	0	0	0	1
Coryphaenoides anguliceps	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coryphaenoides cinereus	1	1	0	1	0	0	1	0	0	1	0	0	1	1
Coryphaenoides zaniophorus	1	1	1	1	1	0	0	1	1	0	0	0	1	1
Caelorinchus caelorhincus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caelorinchus occa	1	1	0	0	0	1	1	0	1	0	0	0	1	1
Macrourus berglax	?	?	?	?	?	?	?	?	?	?	?	?	?	?

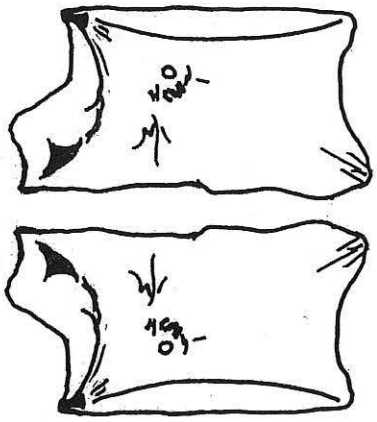
Table 4

Data Matrix of Morphological and Molecular Characters for Rattail Analysis

	113	114	115	116	117	118	119	120
Melanonus zugmayeri	?	?	?	?	?	?	?	?
Hymenocephalus italicus	?	?	?	?	?	?	?	?
Echinomacrurus mollis	?	?	?	?	?	?	?	?
Mataeocephalus microstomus	?	?	?	?	?	?	?	?
Cetonurus globiceps	?	?	?	?	?	?	?	?
Sphagemacrurus hirundo	?	?	?	?	?	?	?	?
Nezumia aequalis	?	?	?	?	?	?	?	?
Trachonurus villosus	?	?	?	?	?	?	?	?
Malacocephalus laevis	?	?	?	?	?	?	?	?
Ventrifossa sp.	?	?	?	?	?	?	?	?
Albatrossia pectoralis	1	1	1	1	0	0	1	0
Lionurus filicauda	?	?	?	?	?	?	?	?
Lionurus carapinus	?	?	?	?	?	?	?	?
Chalinura leptolepis	1	1	1	1	0	0	0	1
Chalinura brevibarbis	?	?	?	?	?	?	?	?
Nematonurus armatus	1	1	1	1	0	0	0	1
Nematonurus yaquinae	?	?	?	?	?	?	?	?
Coryphaenoides rupestris	0	0	1	1	1	1	1	0
Coryphaenoides acrolepis	1	1	0	0	0	0	1	0
Coryphaenoides filifer	1	1	0	0	0	1	1	0
Coryphaenoides guentheri	?	?	?	?	?	?	?	?
Coryphaenoides mexicanus	1	1	1	1	1	1	1	0
Coryphaenoides anguliceps	?	?	?	?	?	?	?	?
Coryphaenoides cinereus	1	1	0	0	0	1	1	0
Coryphaenoides zaniophorus	1	1	1	0	0	1	1	0
Caelorinchus caelorhincus	?	?	?	?	?	?	?	?
Caelorinchus occa	0	0	1	0	0	1	1	1
Macrourus berglax	?	?	?	?	?	?	?	?

Table 4

A



B

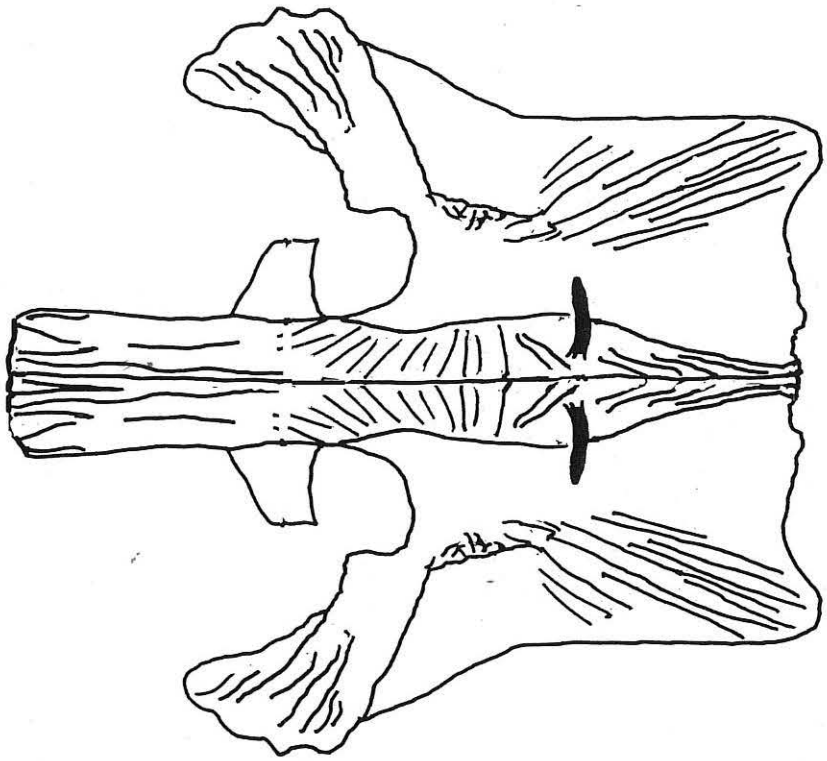
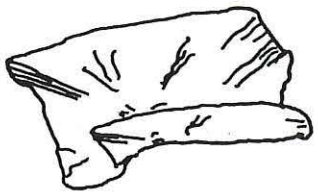


Figure 1. Nasals, dorsal (x6).

Figure 1A. *Chalinura leptolepis*, composite CS2:5 and CS6:1.

Figure 1B. *Caelorinchus c. caelorhincus*, CS4:7.

A



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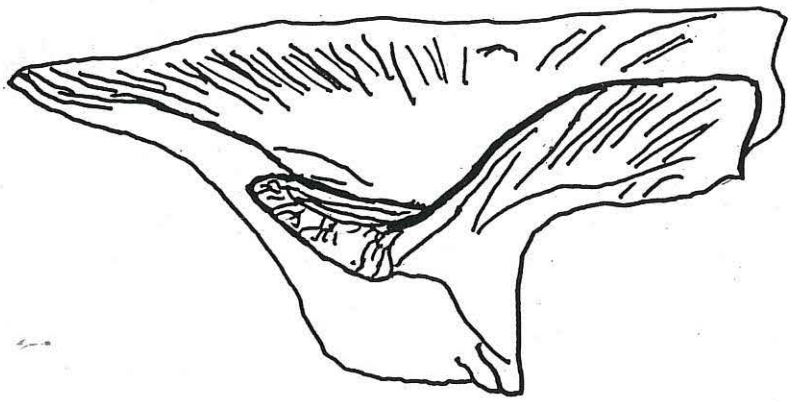
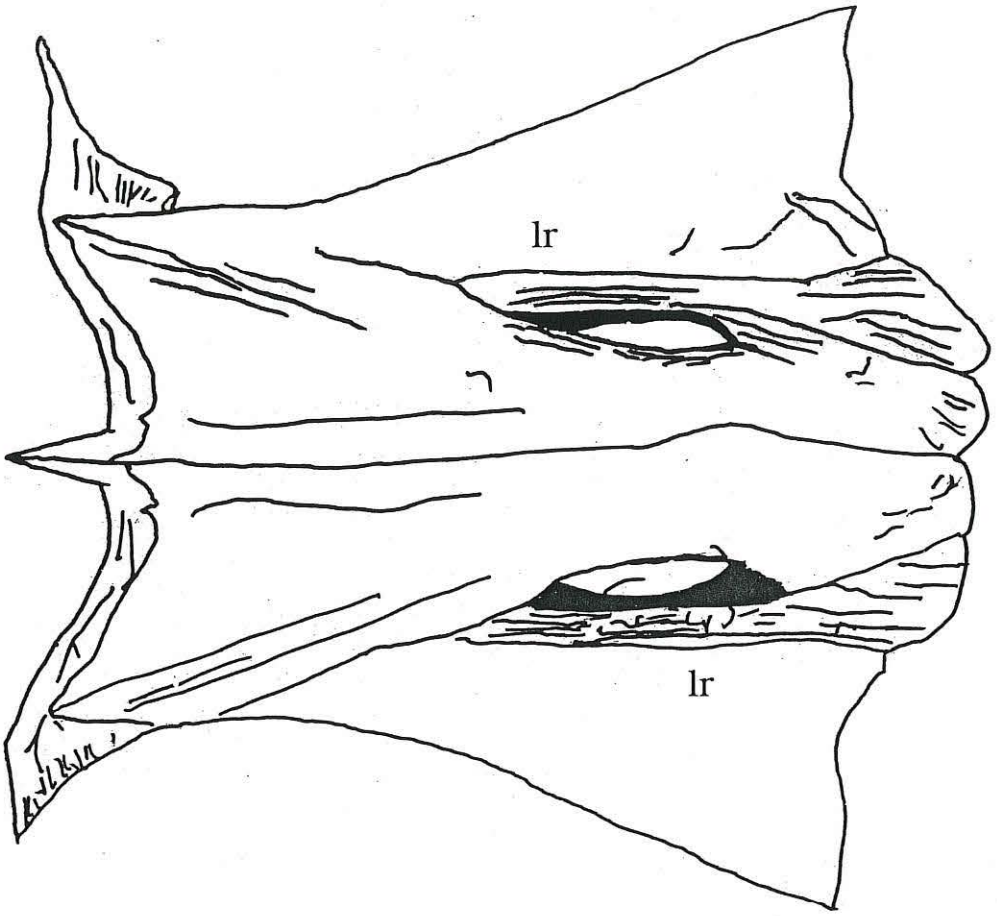


Figure 2. Nasals, left lateral (x6).

Figure 2A. *Chalinura leptolepis*, CS2:5.

Figure 2B. *Caelorinchus c. caelorhincus*, CS4:7.

A



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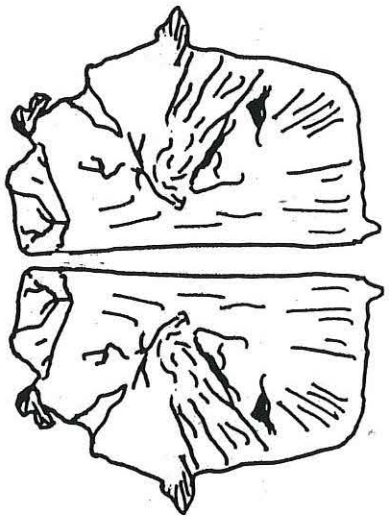


Figure 3. Frontals, dorsal (x6).

Figure 3A. *Caelorinchus c. caelorhincus*, CS4:7.

Figure 3B. *Coryphaenoides rupestris*, CS2:1.

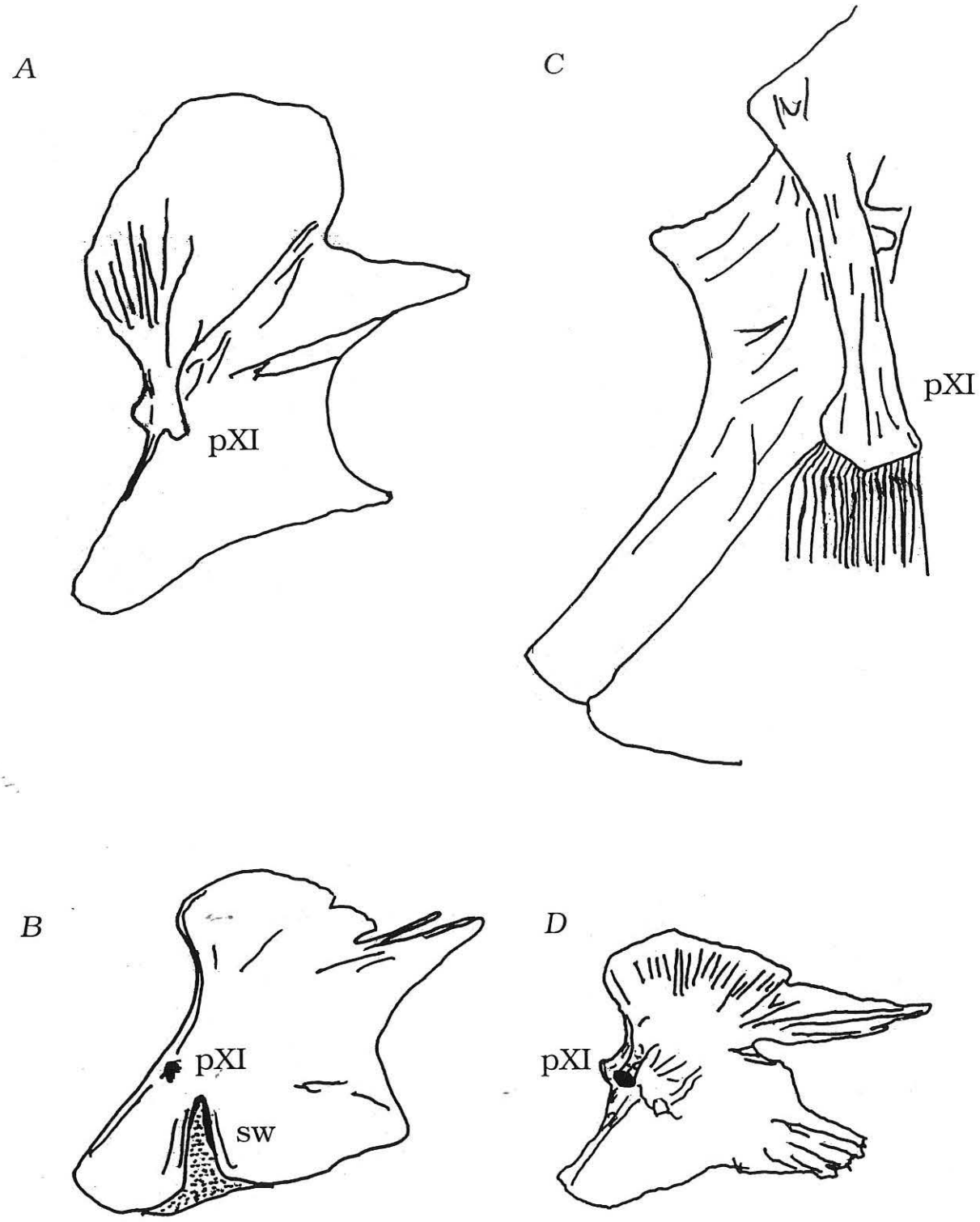


Figure 4. Mesethmoid (x12).

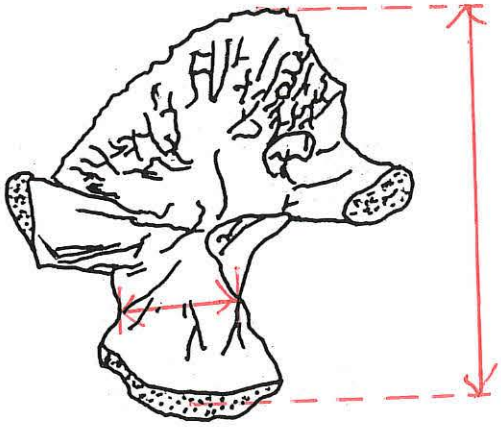
Figure 4A. Left anterolateral *Coryphaenoides guentheri*, CS2:2.

Figure 4B. Left lateral *Malacocephalus laevis*, CS7:3.

Figure 4C. Left anterolateral *Coryphaenoides zaniophorus*, CS9:1.

Figure 4D. Left lateral *Nematonurus armatus*, CS4:3.

A



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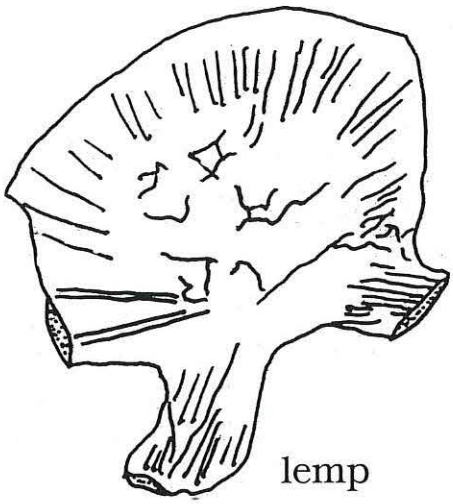


Figure 5. Left lateral ethmoid, posterior.

Figure 5A. (x12) *Nematonurus armatus*, CS4:3.

Figure 5B. (x6) *Macrourus berglax*, CS7:4.

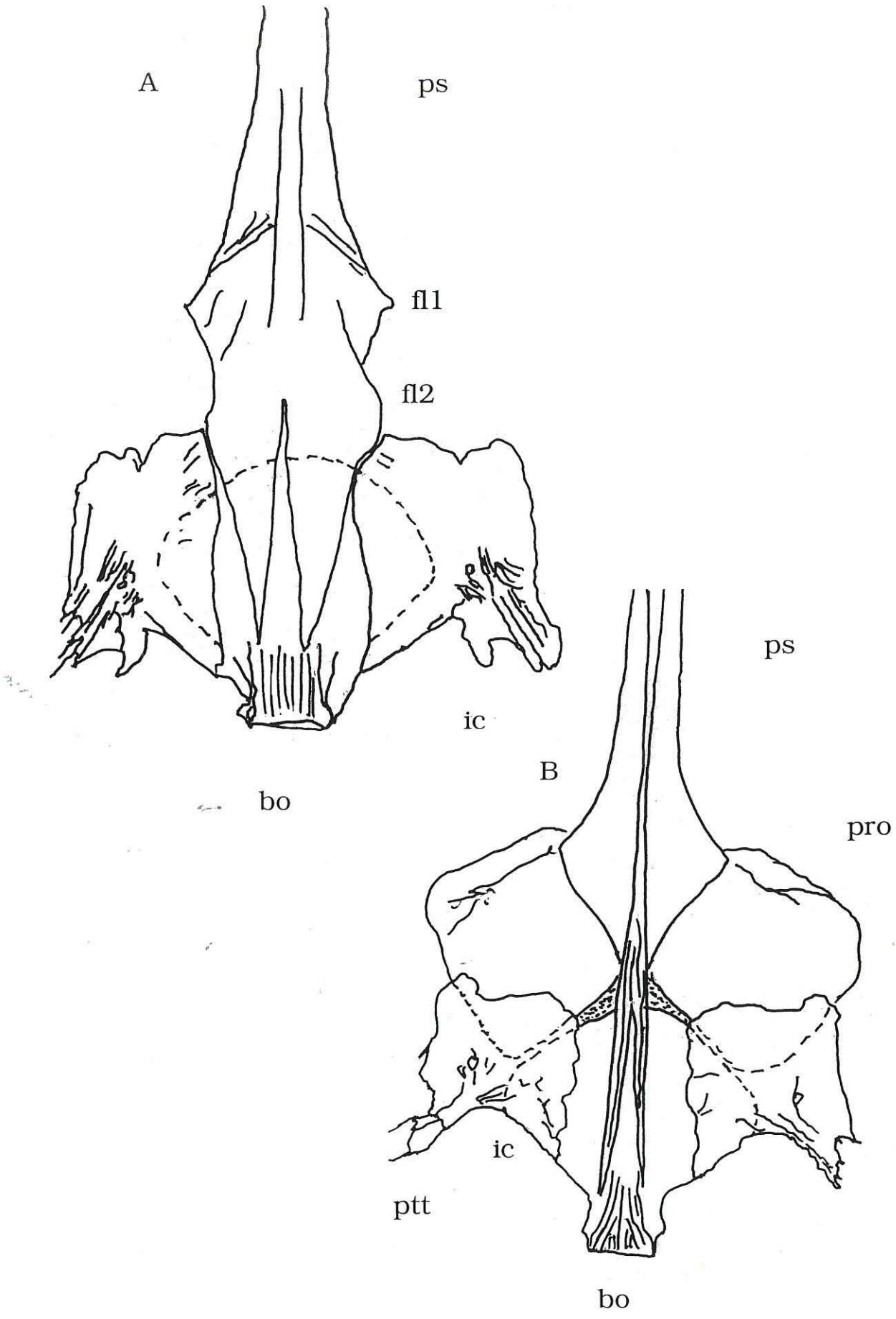
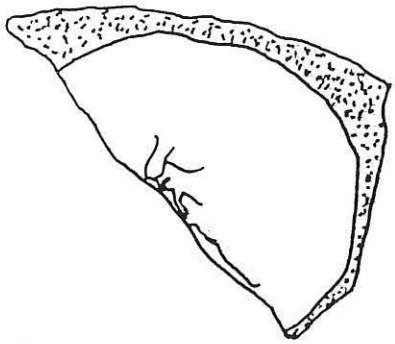


Figure 6. Parasphenoid and surrounding bones, ventral (x6).

Figure 6A. *Malacocephalus laevis*, CS4:6.

Figure 6B. *Caelorinchus c. caelorhincus*, CS4:7.

A



B

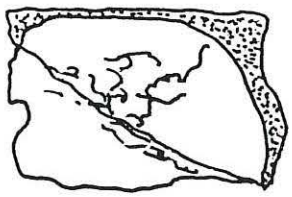


Figure 7. Pterosphenoid, left lateral (x12).

Figure 7A. *Coryphaenoides rupestris*, CS**1**:1.

Figure 7B. *Nematonurus armatus*, CS**4**:3.

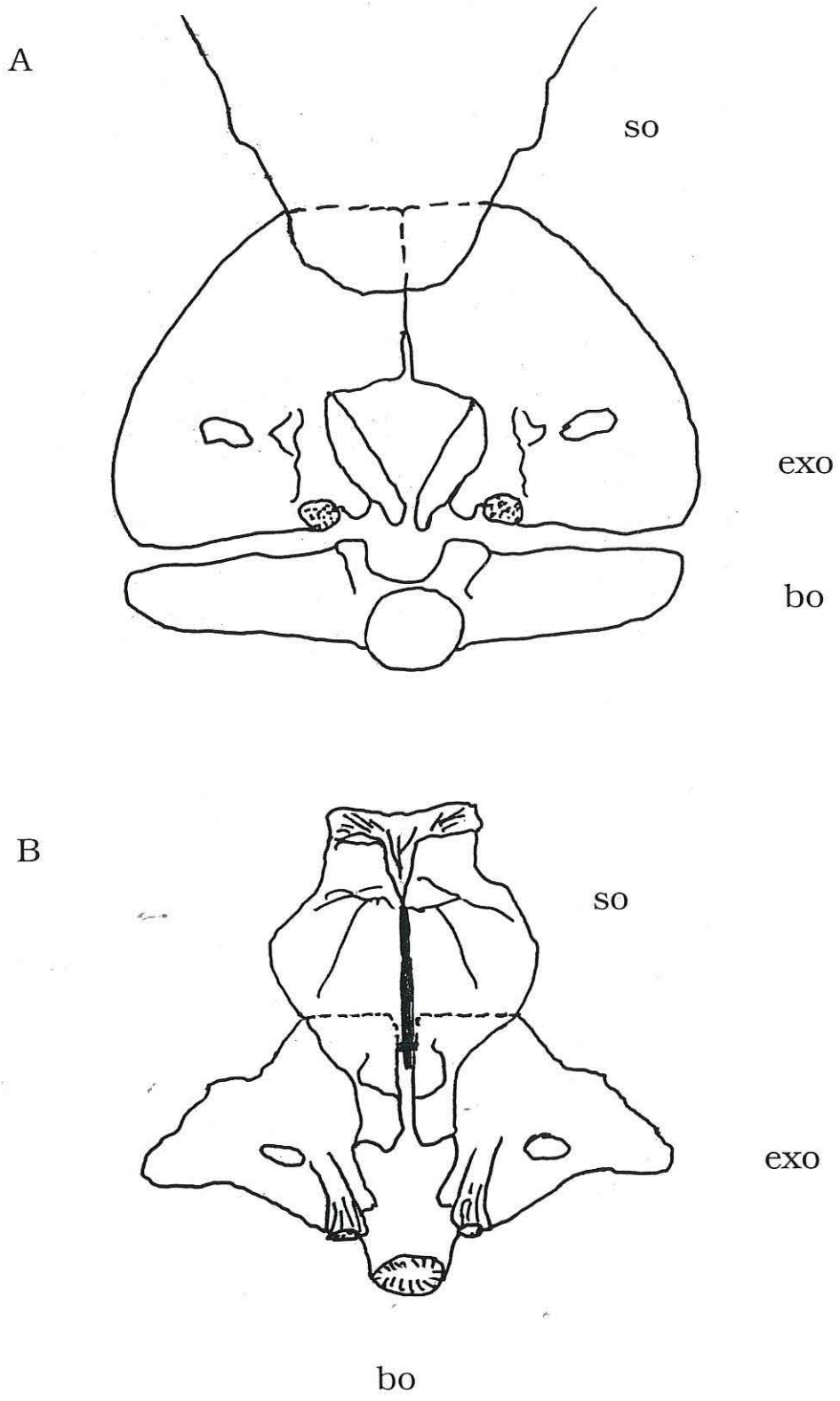


Figure 8. Occipital region.

Figure 8A. Posterior (x12) *Coryphaenoides rupestris*, CS1:1.

Figure 8B. Dorsoposterior (x6) *Caelorinchus c. caelorhincus*, CS4:7.

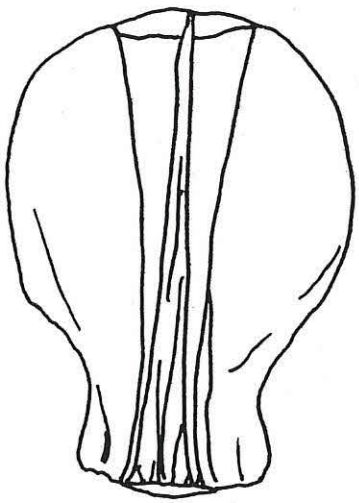


Figure 9. Basioccipital, ventral (x12) *Lionurus filicauda*, CS2:3.

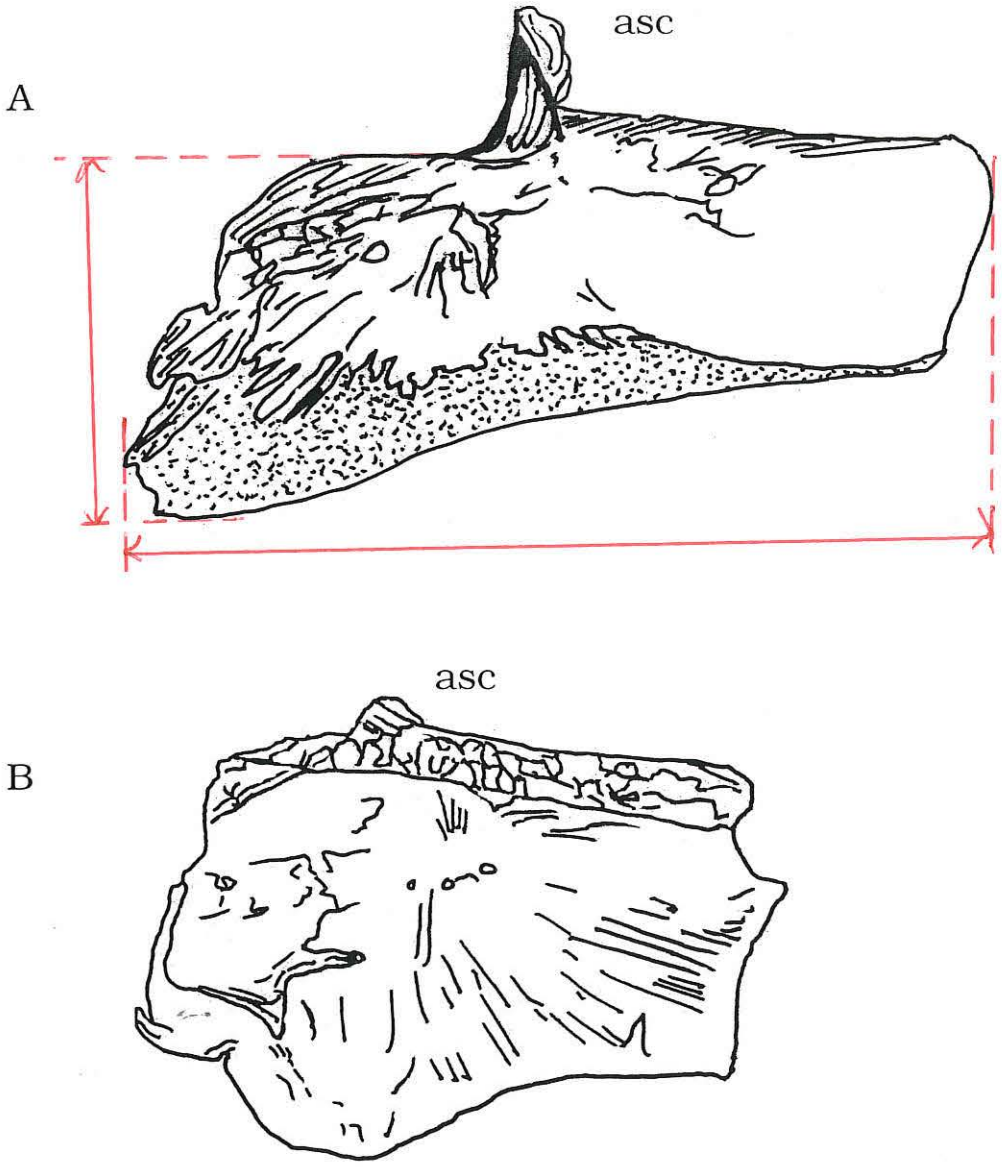


Figure 10. First infraorbital, left lateral (x6).

Figure 10A. *Nematonurus yaquinae*, CS**8**:2.

Figure 10B. *Caelorinchus c. caelorhincus*, CS**4**:7.

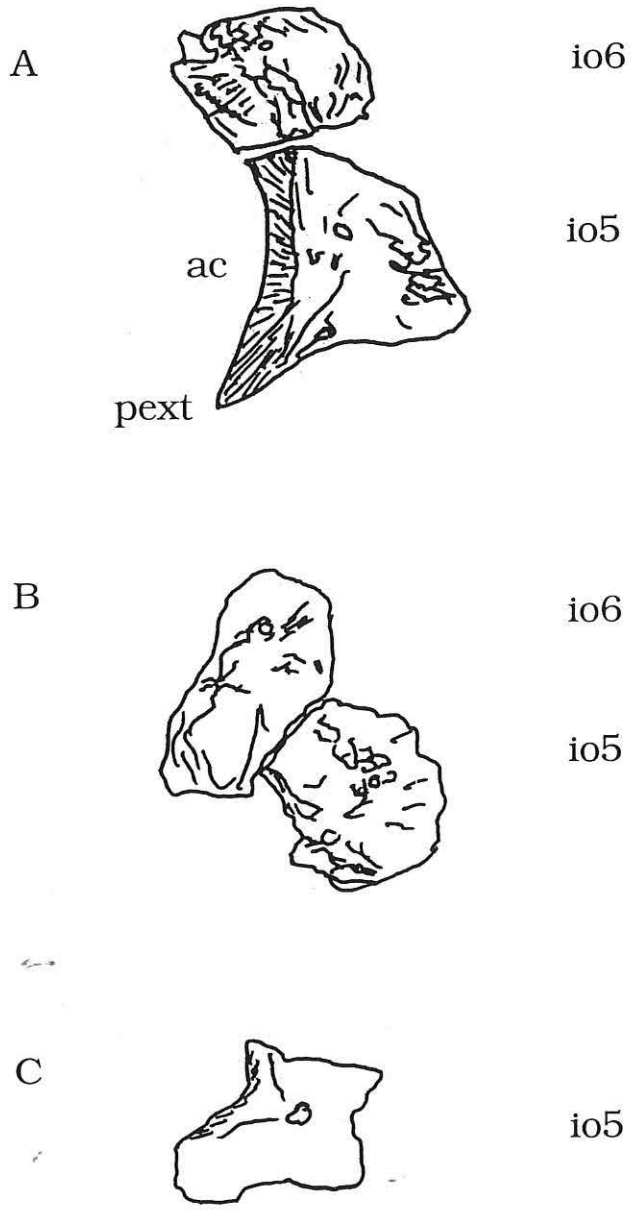


Figure 11. Fifth and sixth infraorbitals, left lateral (x6).

Figure 11A. *Coryphaenoides guentheri*, CS2:2.

Figure 11B. *Lionurus carapinus*, CS2:4.

Figure 11C. *Chalinura leptolepis*, CS6:1.

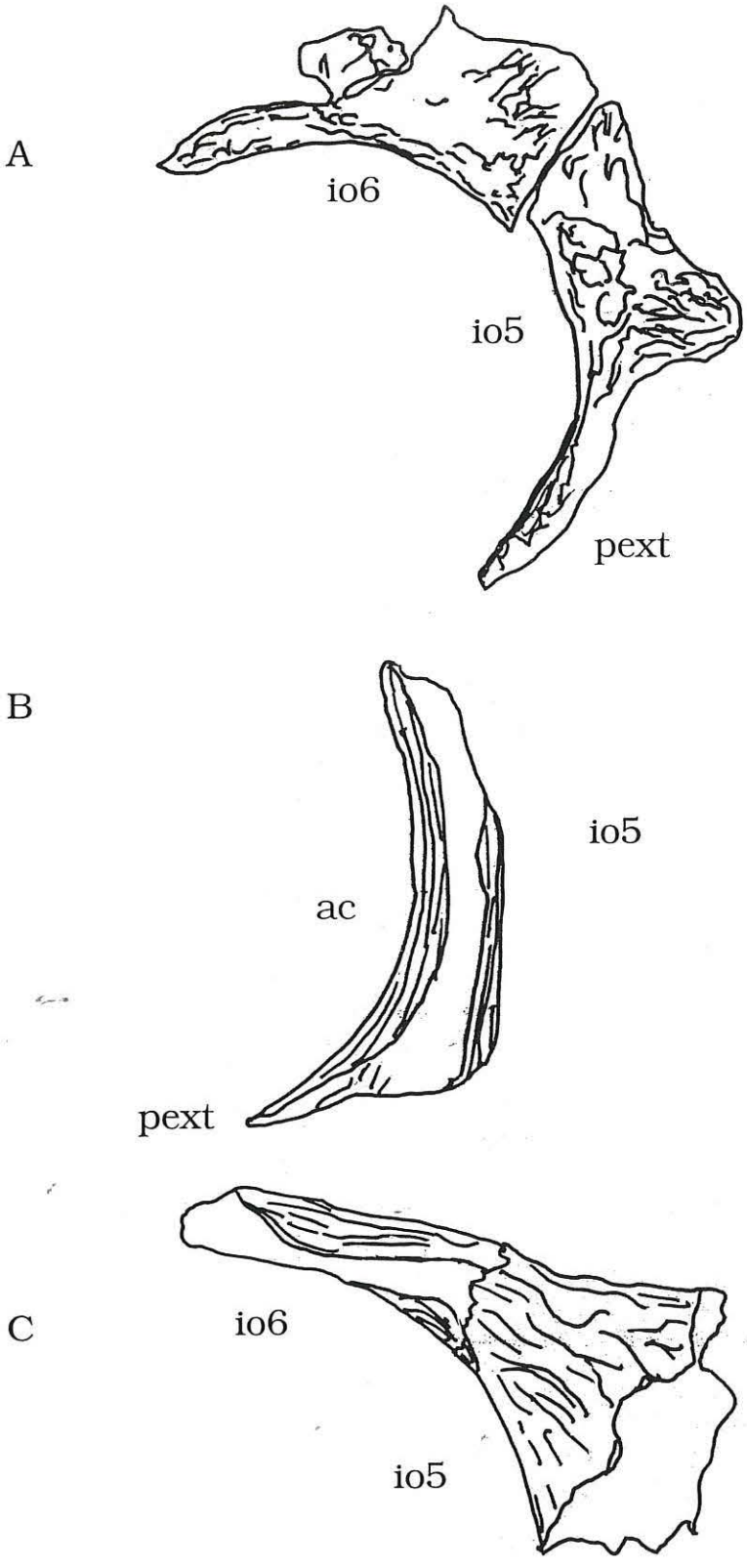


Figure 12. Fifth and sixth infraorbitals, left lateral.

Figure 12A. (x12) *Melanonus zugmayeri*, GJH.

Figure 12B. (x6) *Macrourus berglax*, CS7:4.

Figure 12C. (x6) *Malacocephalus laevis*, SK3.

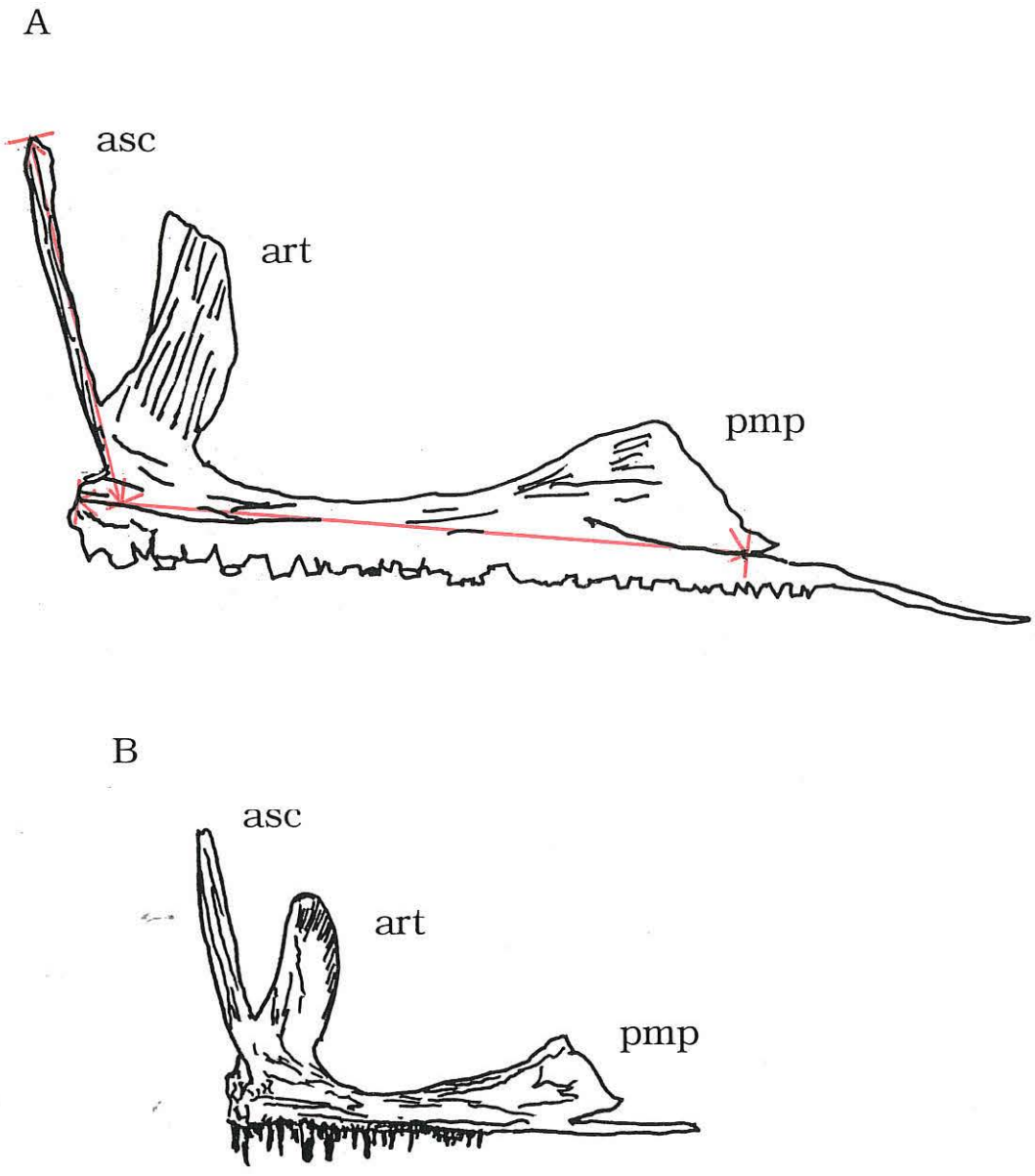


Figure 13. Premaxilla, left lateral.

Figure 13A. (x6) *Nematonurus yaquinae*, CS8:2.

Figure 13B. (x12) *Coryphaenoides guentheri*, CS2:2.

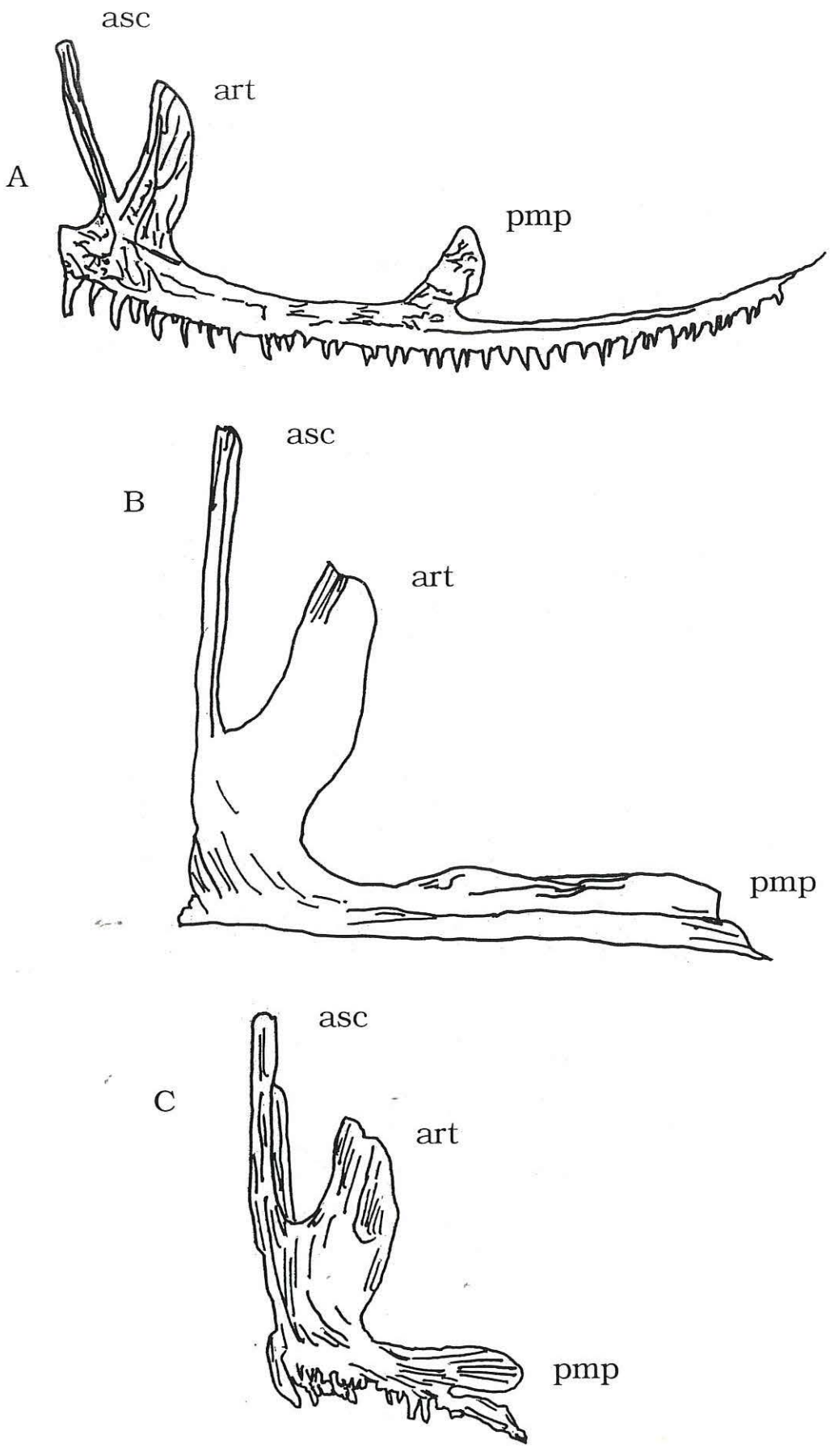


Figure 14. Premaxilla, left lateral.

Figure 14A. (x12) *Melanonus zugmayeri*, GJH.

Figure 14B. (x6) *Coryphaenoides zaniophorus*, CS**9**:1.

Figure 14C. (x6) *Macrourus berglax*, CS**7**:4.

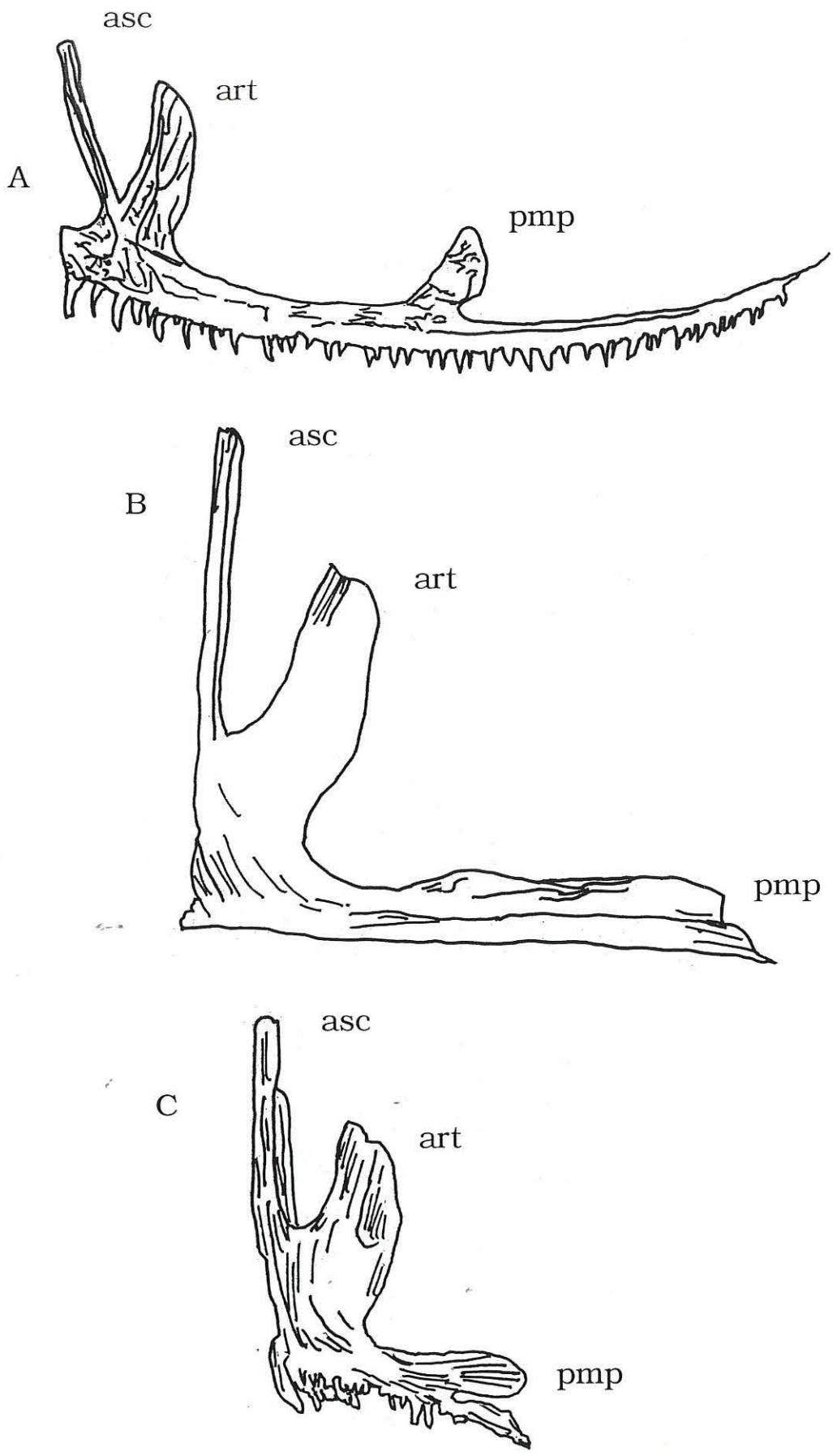


Figure 14. Premaxilla, left lateral.

Figure 14A. (x12) *Melanonus zugmayeri*, GJH.

Figure 14B. (x6) *Coryphaenoides zaniophorus*, CS9:1.

Figure 14C. (x6) *Macrourus berglax*, CS7:4.

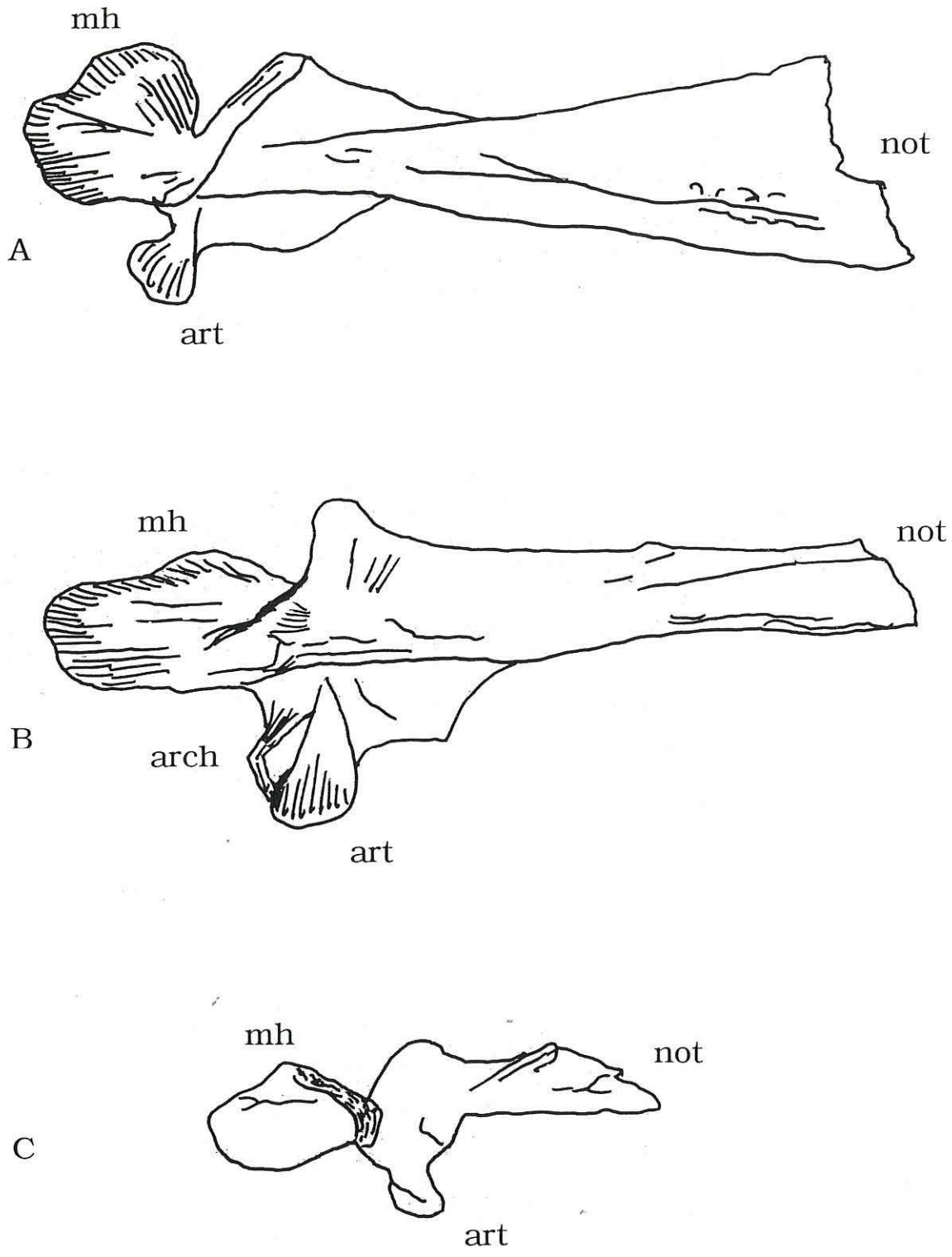


Figure 15. Left maxilla.

Figure 15A. Dorsal (x12) *Lionurus filicauda*, CS2:3.

Figure 15B. Dorsal (x6) *Caelorinchus c. caelorhincus*, CS4:7.

Figure 15C. Ventral (x6) *Mataeocephalus microstomus*, CS4:8.

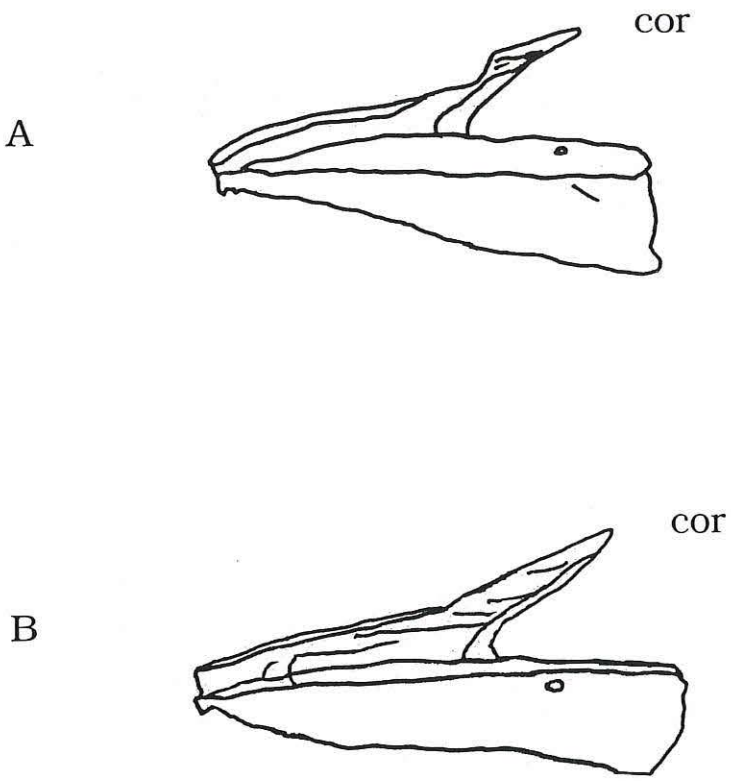


Figure 16. Dentary, left lateral (x6).

Figure 16A. *Coryphaenoides rupestris*, CS2:1.

Figure 16B. *Lionurus filicauda*, CS2:3.

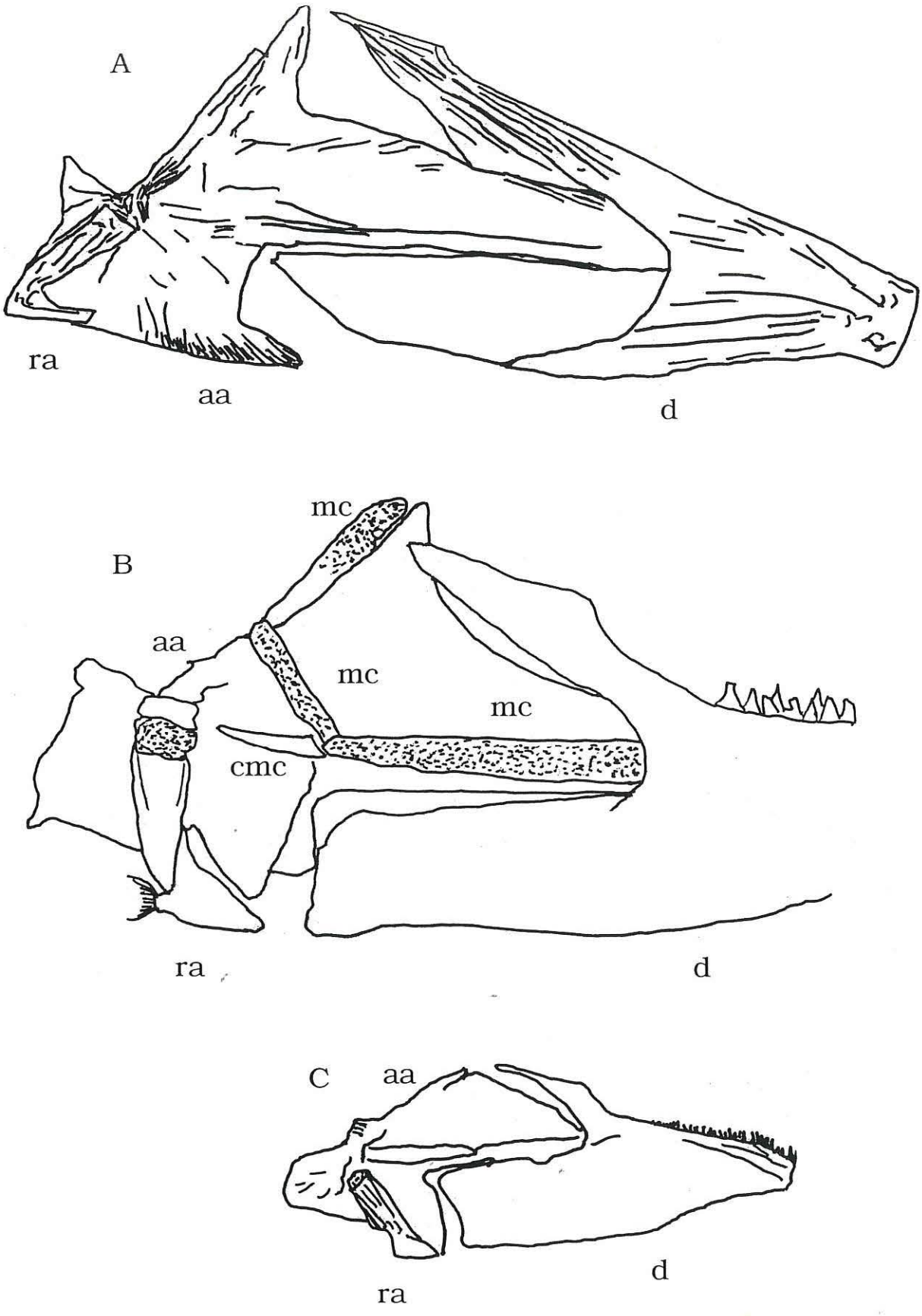


Figure 17. Lower jaw, left medial.

Figure 17A. (x6) *Melanonus zugmayeri*, GJH.

Figure 17B. (x12) *Coryphaenoides rupestris*, CS1:1.

Figure 17C. (x6) *Caelorinchus c. caelorhincus*, CS4:7.

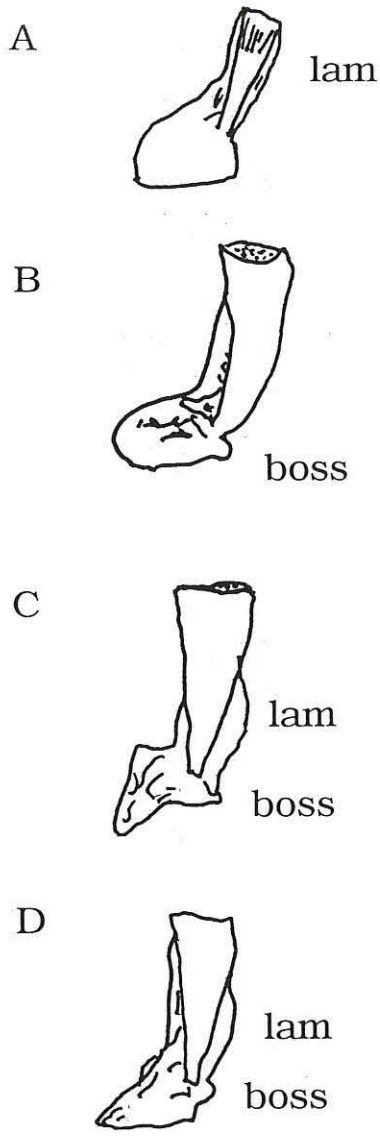


Figure 18. Retroarticular, left lateral (x12).

Figure 18A. *Coryphaenoides guentheri*, CS2:2.

Figure 18B. *Chalinura leptolepis*, CS2:5.

Figure 18C. *Lionurus filicauda*, CS2:3.

Figure 18D. *Coryphaenoides rupestris*, CS2:1.

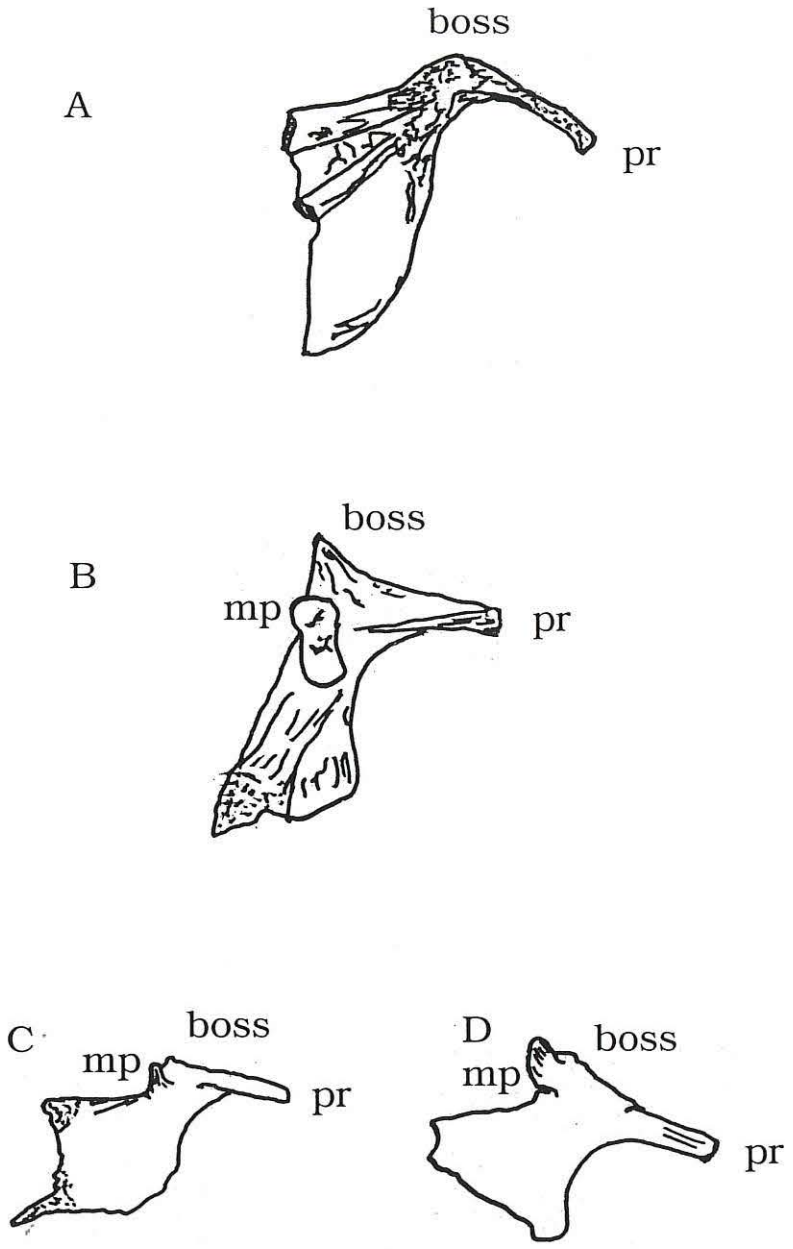


Figure 19. Palatine, left medial.

Figure 19A. (x12) *Hymenocephalus italicus*, CS2:2.

Figure 19B. (x12) *Sphagemacrurus hirundo*, CS4:4.

Figure 19C. (x3) *Chalinura brevibarbis*, CS8:1.

Figure 19D. (x3) *Coryphaenoides anguliceps*, CS9:7.

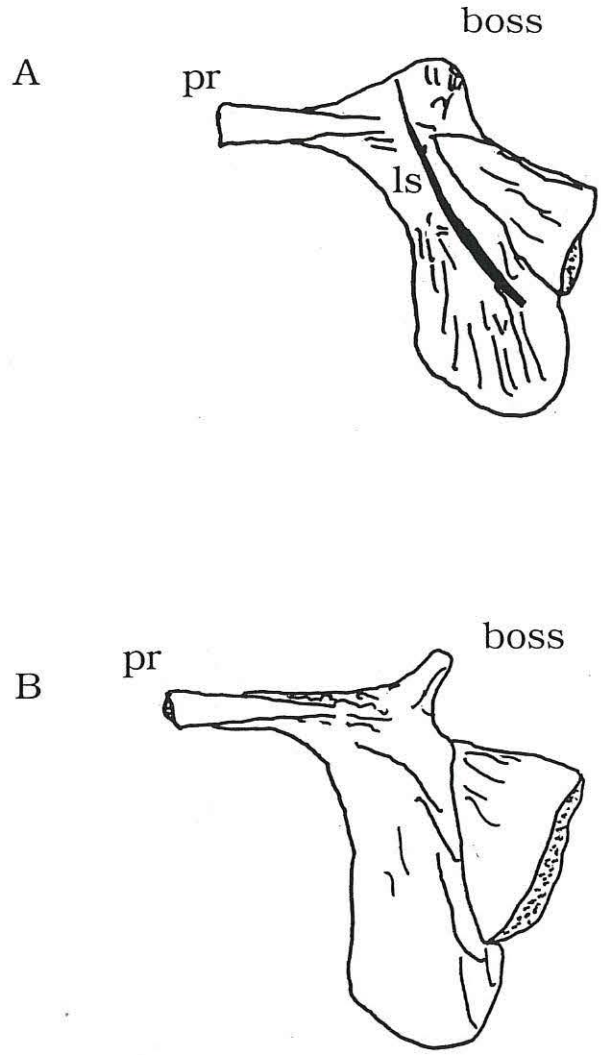
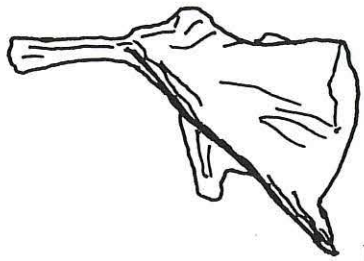


Figure 20. Palatine, left lateral (x12).

Figure 20A. *Coryphaenoides rupestris*, CS2:1.

Figure 20B. *Lionurus filicauda*, CS2:3.

A



B

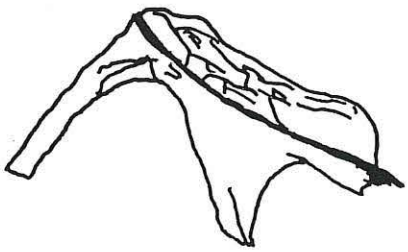


Figure 21. Palatine (x12).

Figure 21A. Left dorsolateral, *Malacocephalus laevis*, CS7:3.

Figure 21B. Left lateral, *Ventrifossa sp.*, GJH.

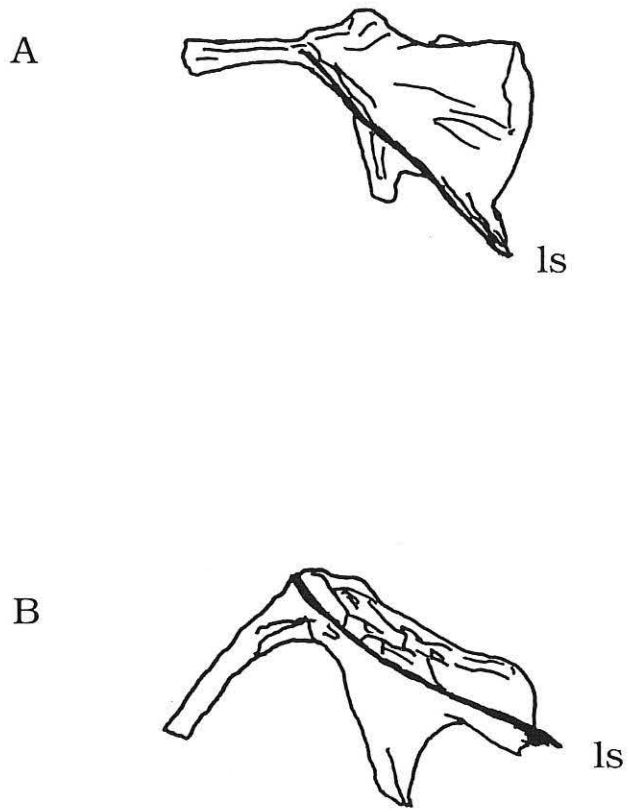


Figure 21. Palatine (x12).

Figure 21A. Left dorsolateral, *Malacocephalus laevis*, CS7:3.

Figure 21B. Left lateral, *Ventrifossa sp.*, GJH.

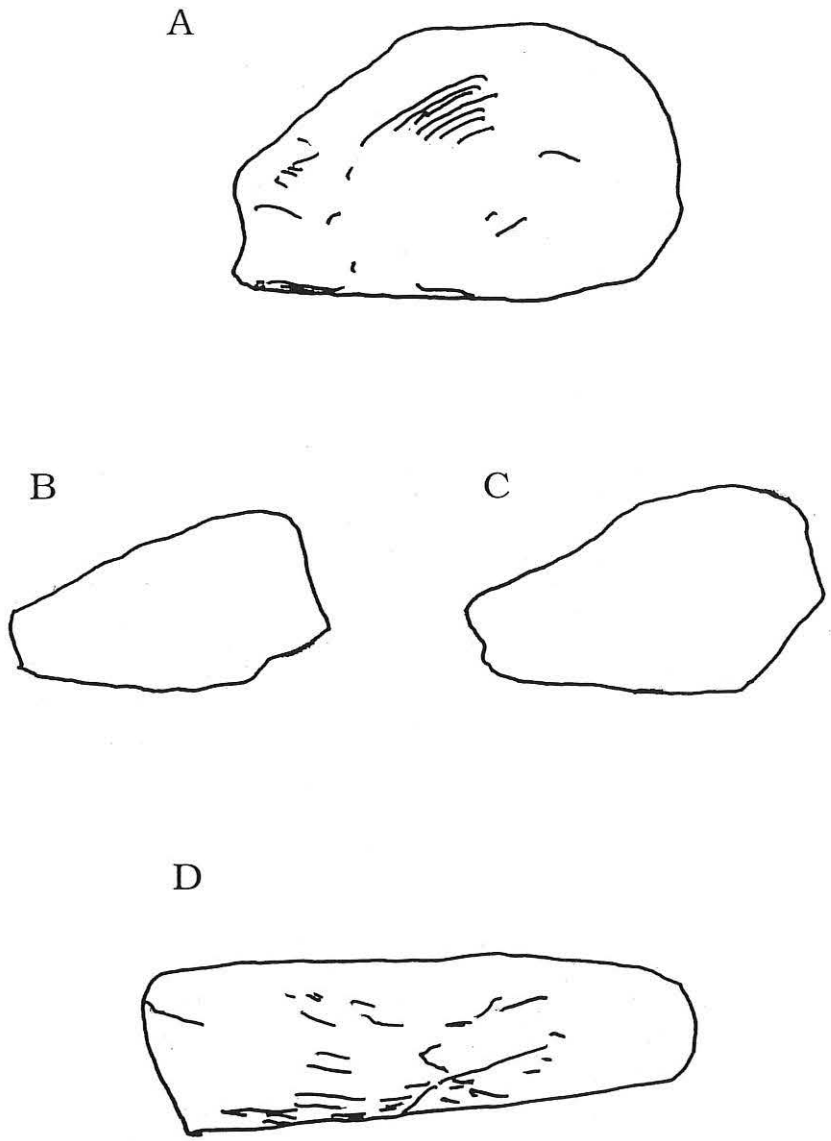


Figure 22. Entopterygoid, left lateral.

Figure 22A. (x12) *Coryphaenoides rupestris*, CS2:1.

Figure 22B. (x6) *Trachonurus villosus*, GJH.

Figure 22C. (x6) *Ventrifossa sp.*, GJH.

Figure 22D. (x12) *Chalinura leptolepis*, CS2:5.

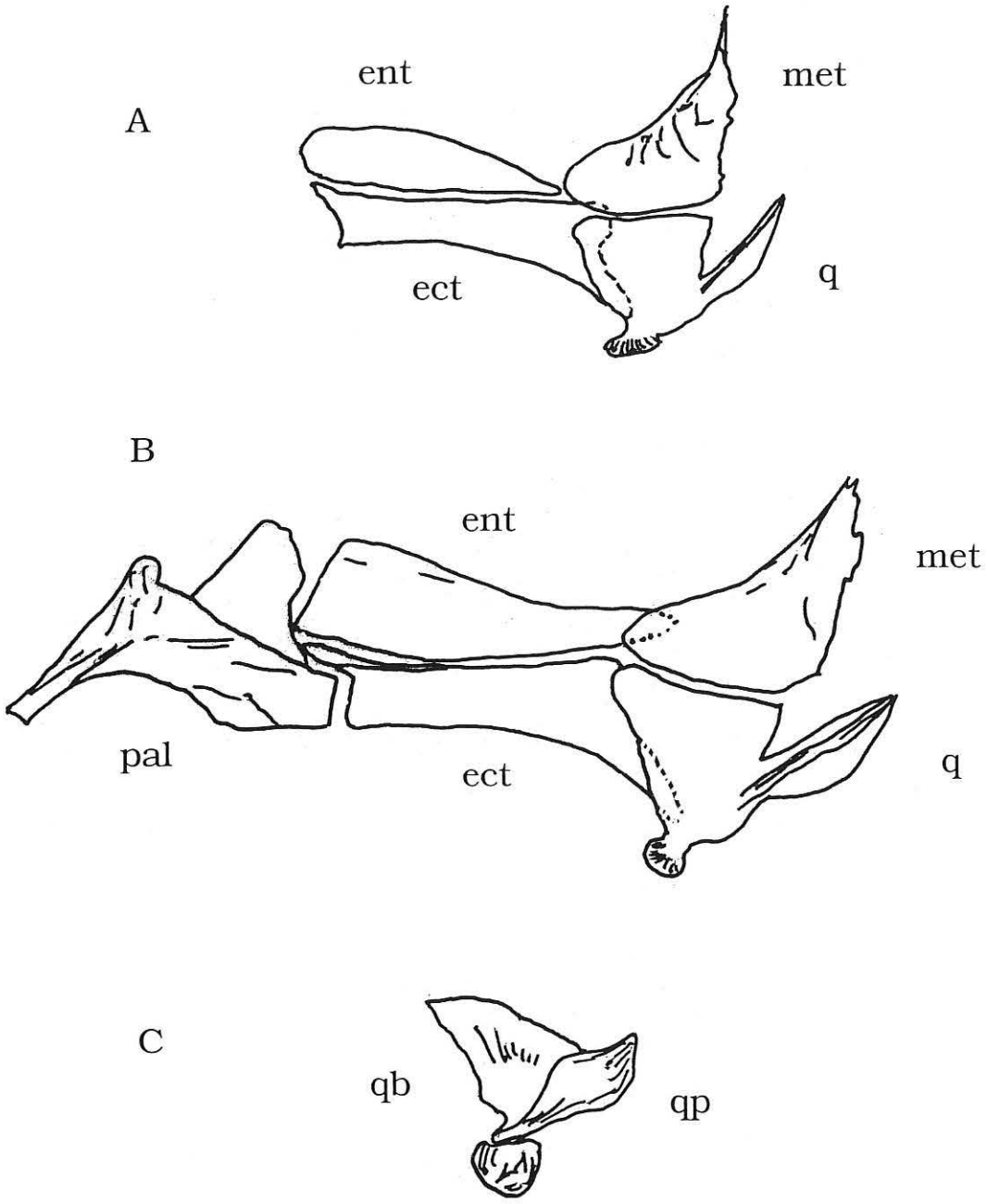


Figure 23. Palatopterygoquadrate, left lateral.

Figure 23A. (x6) *Nematonurus armatus*, CS4:3.

Figure 23B. (x12) *Lionurus carapinus*, CS2:4.

Figure 23C. (x6) *Macrourus berglax*, CS7:4.

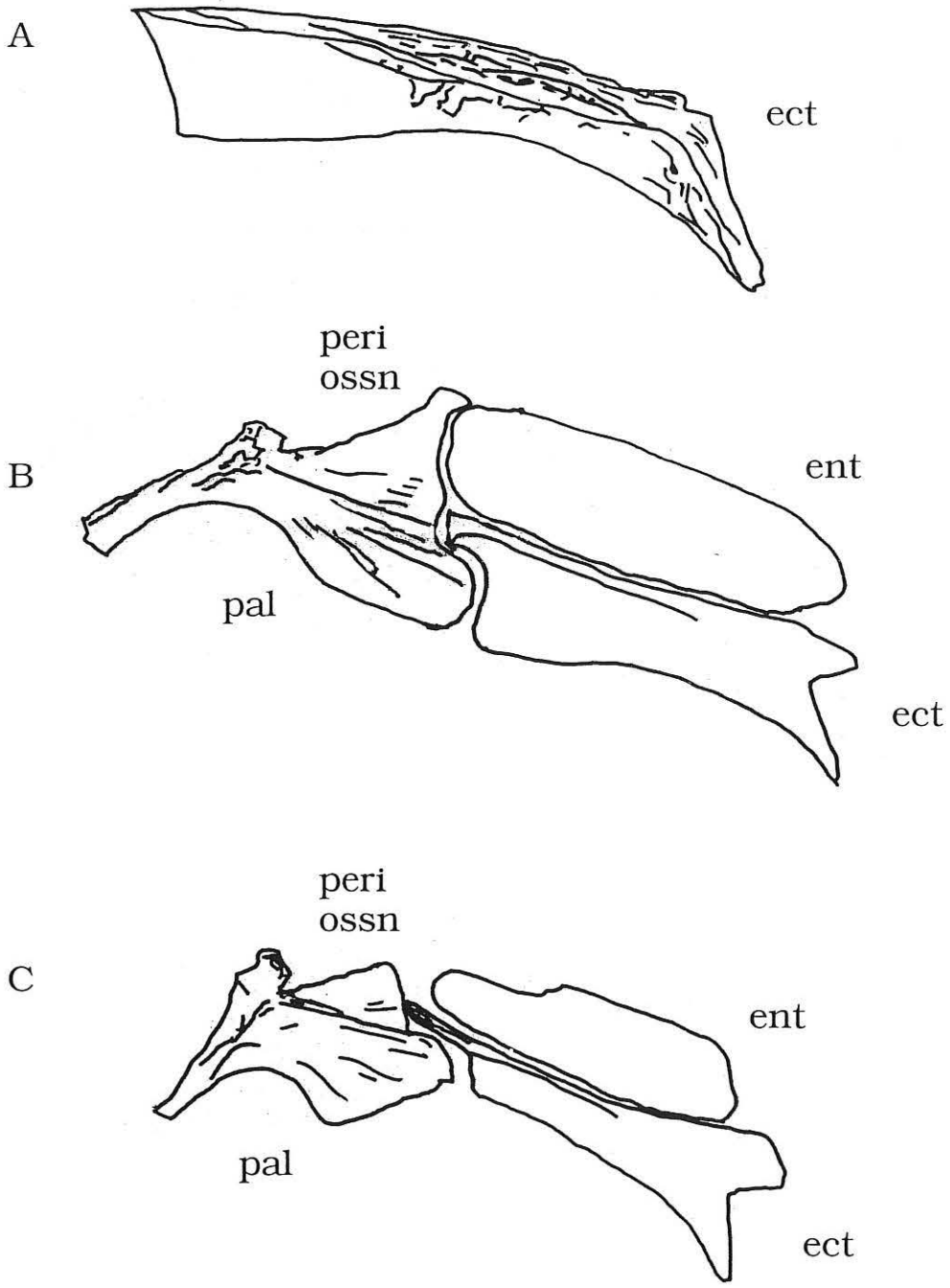


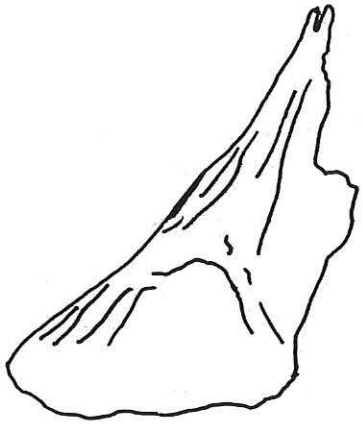
Figure 24. Palatine and pterygoids, left lateral.

Figure 24A. (x12) *Hymenocephalus italicus*, CS2:6.

Figure 24B. (x6) *Chalinura leptolepis*, CS6:1.

Figure 24C. (x3) *Coryphaenoides anguliceps*, CS9:7.

A



B

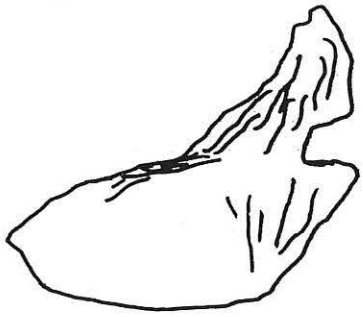


Figure 25. Metapterygoid, left lateral (x6).

Figure 25A. *Coryphaenoides mexicanus*, CS**9**:8.

Figure 25B. *Chalinura leptolepis*, CS**6**:1.

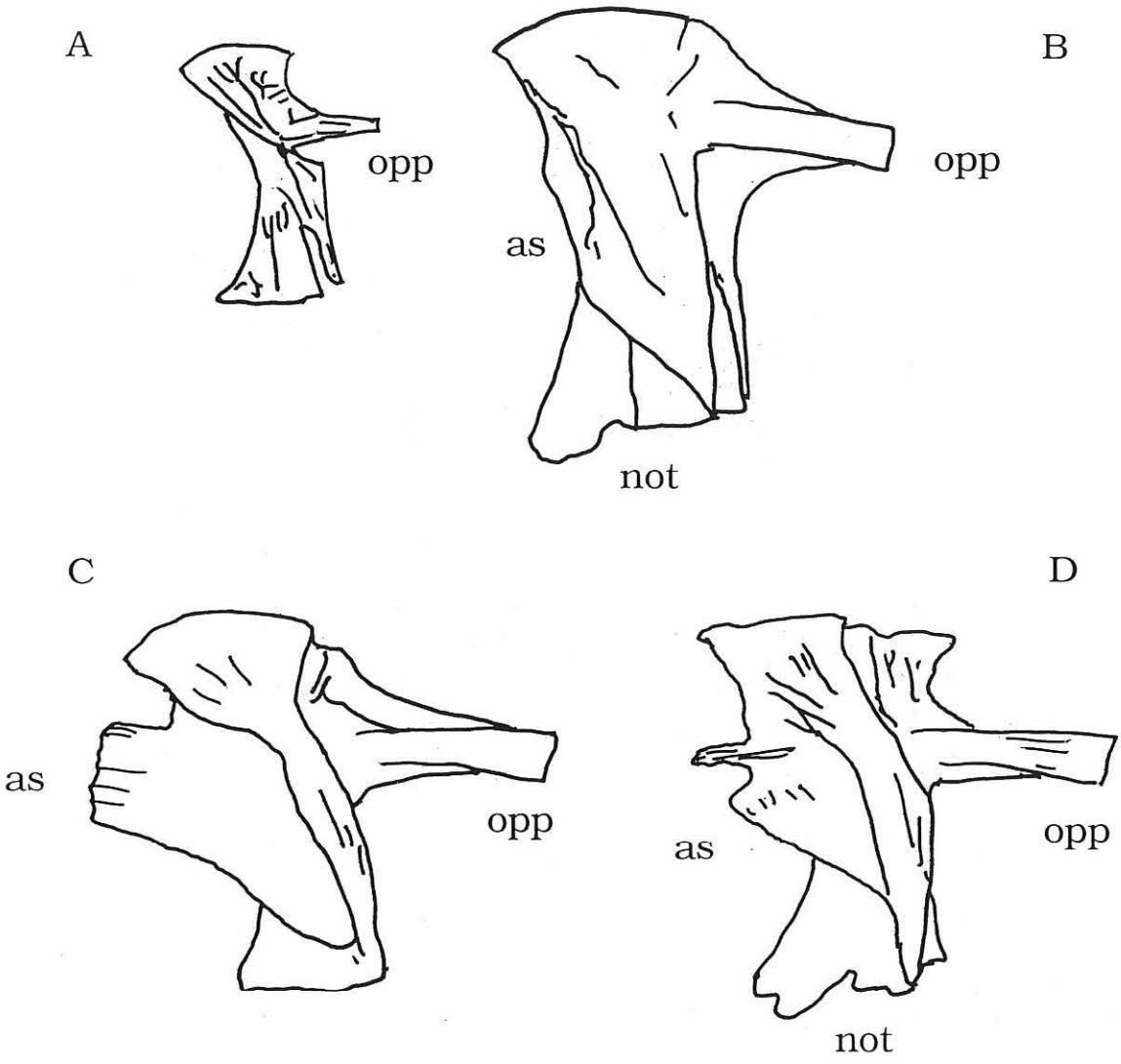


Figure 26. Hyomandibula, left lateral.

Figure 26A. (x6) *Melanonus zugmayeri*, GJH.

Figure 26B. (x12) *Coryphaenoides rupestris*, CS2:1.

Figure 26C. (x12) *Chalinura leptolepis*, CS6:1.

Figure 26D. (x12) *Chalinura brevibarbis*, CS8:1.

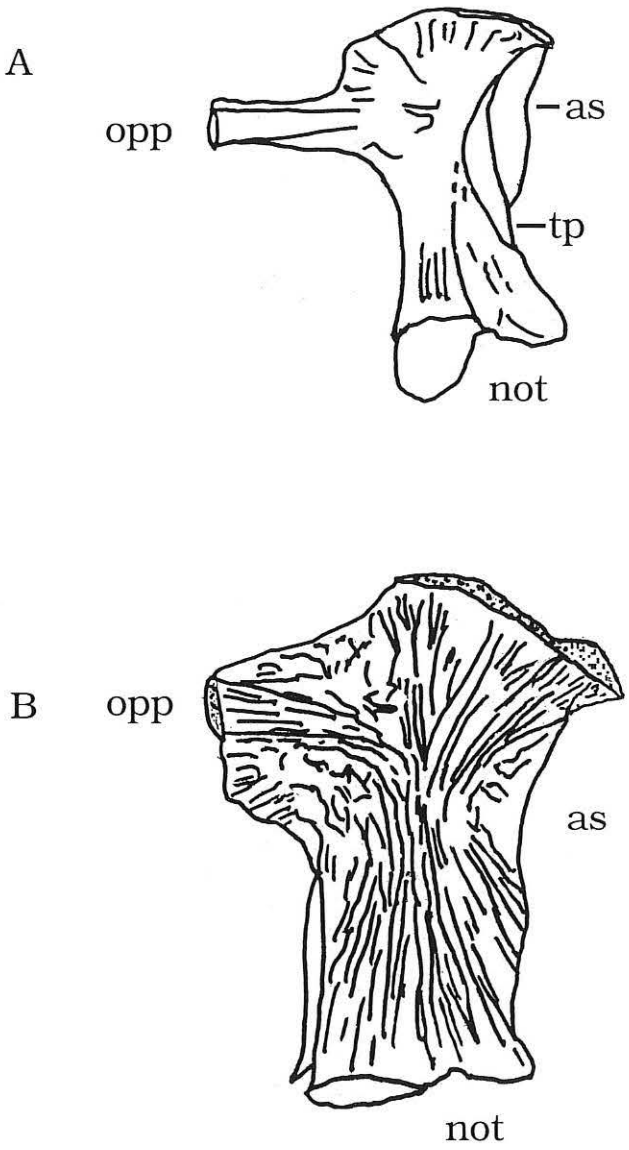


Figure 27. Hyomandibula, left medial.

Figure 27A. (x12) *Coryphaenoides guentheri*, CS2:2.

Figure 27B. (x6) *Macrourus berglax*, CS7:4.

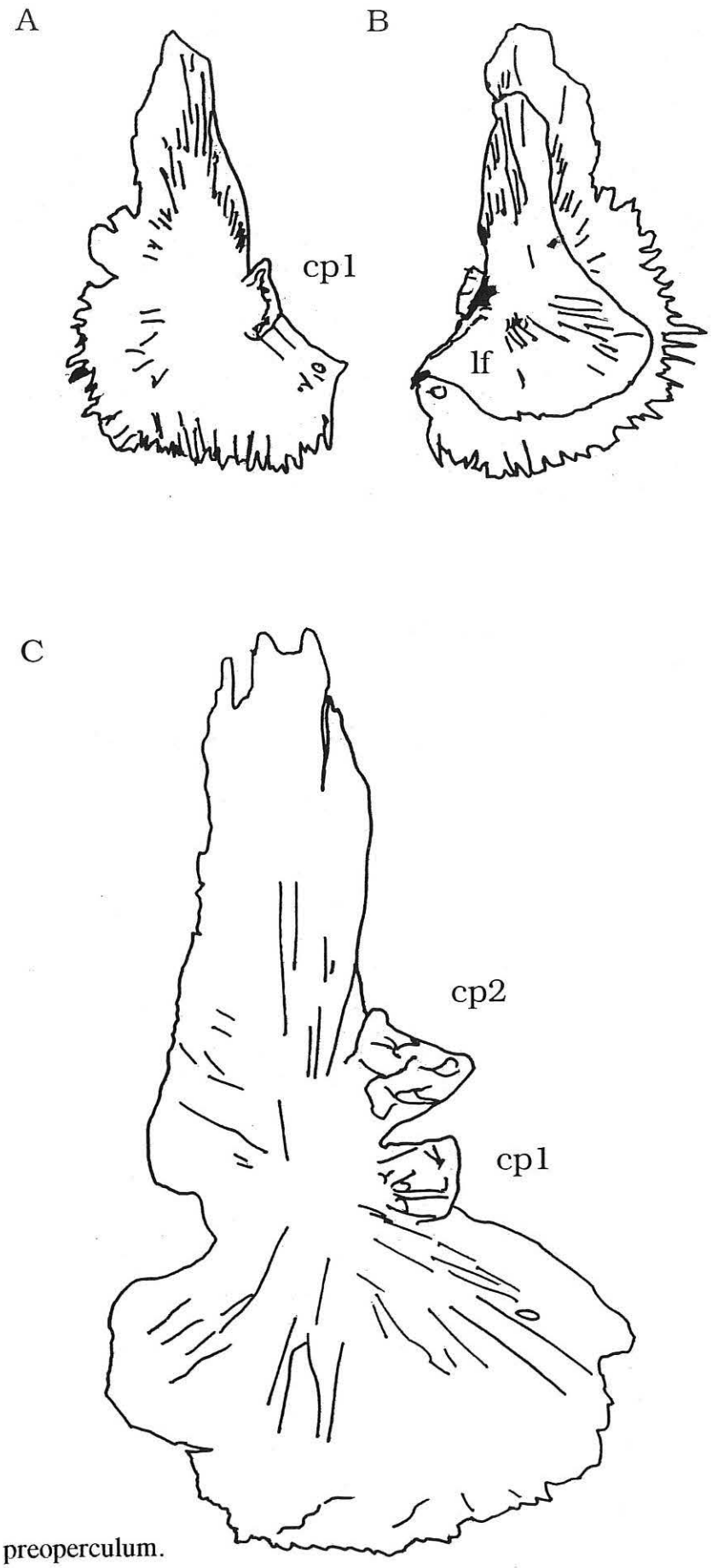


Figure 28. Left preoperculum.

Figure 28A,B. Medial, lateral (x6) *Nematonurus armatus*, CS6:3.

Figure 28C. Medial (x12) *Malacocephalus laevis*, CS4:6.

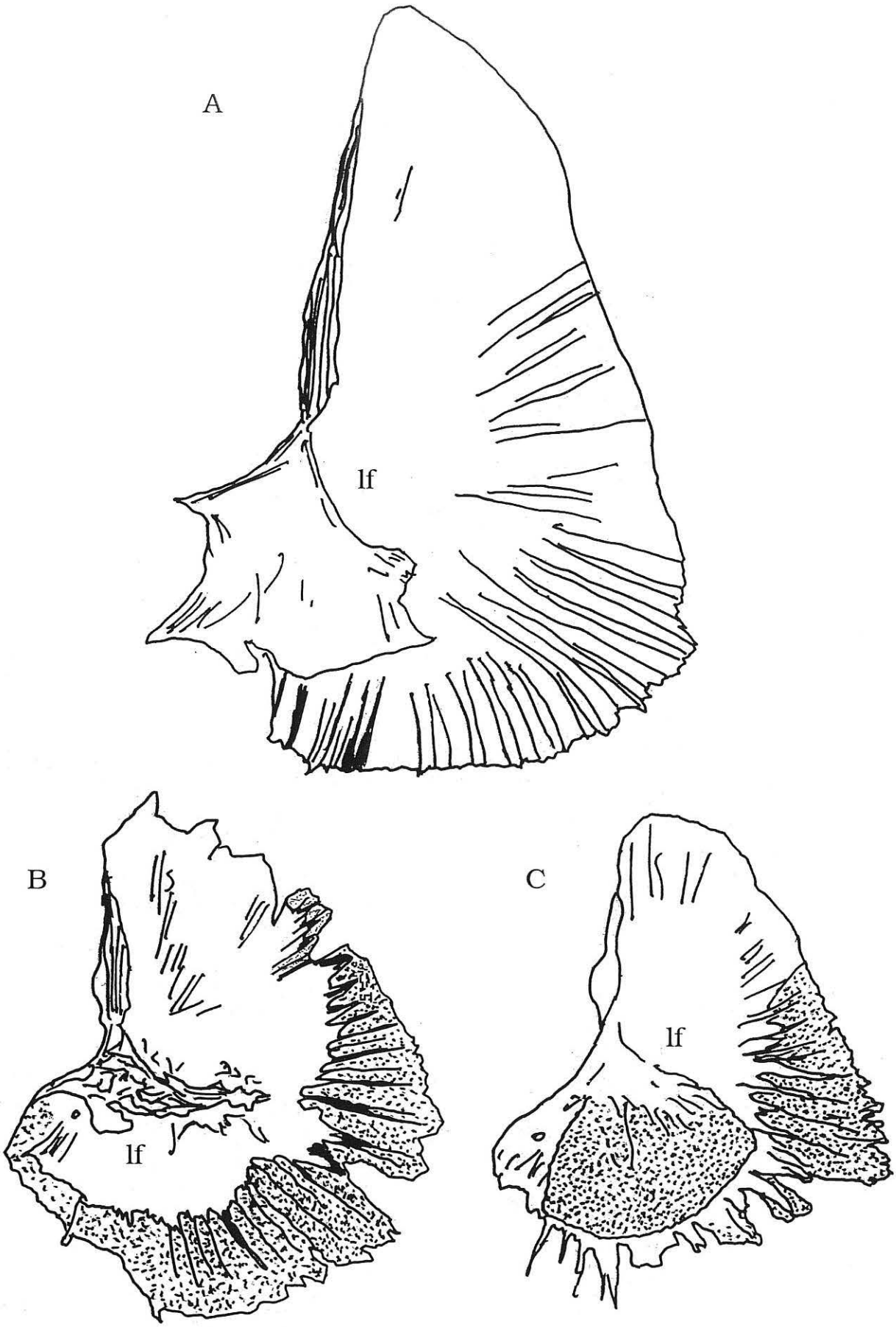


Figure 29. Preoperculum, left lateral.

Figure 29A. (x6) *Coryphaenoides rupestris*, CS5:1.

Figure 29B. (x12) *Coryphaenoides guentheri*, CS2:2.

Figure 29C. (x12) *Lionurus carapinus*, CS2:4.

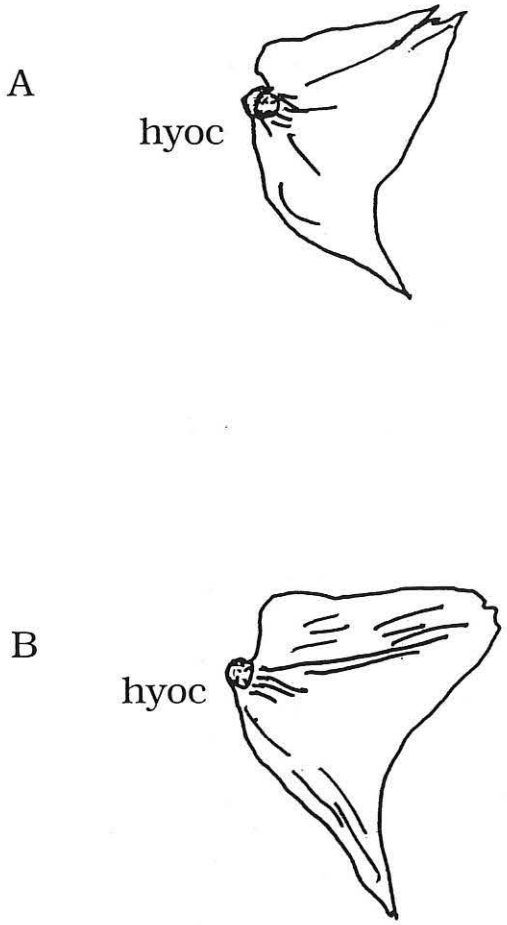


Figure 30. Operculum, left lateral (x6).

Figure 30A. *Nezumia aequalis*, GJH.

Figure 30B. *Trachonurus villosus*, GJH.

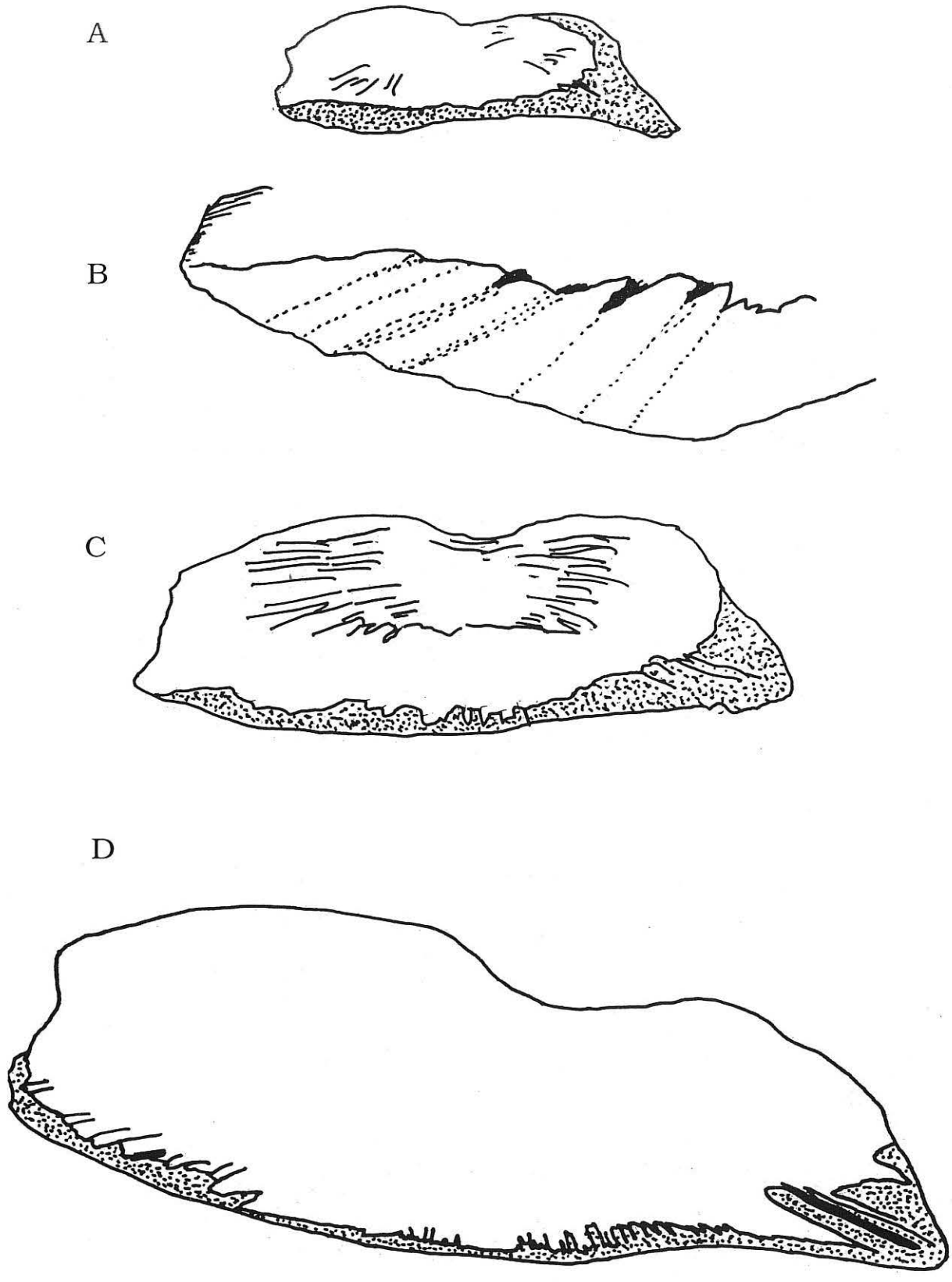


Figure 31. Interoperculum, left lateral.

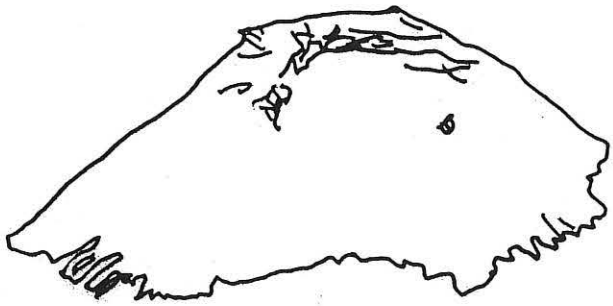
Figure 31A. (x6) *Coryphaenoides guentheri*, CS2:2.

Figure 31B. Anteroventral portion (x25) *Coryphaenoides guentheri*, CS2:2.

Figure 31C. (x6) *Coryphaenoides mexicanus*, CS9:8.

Figure 31D. (x6) *Coryphaenoides anguliceps*, CS9:7.

A



B

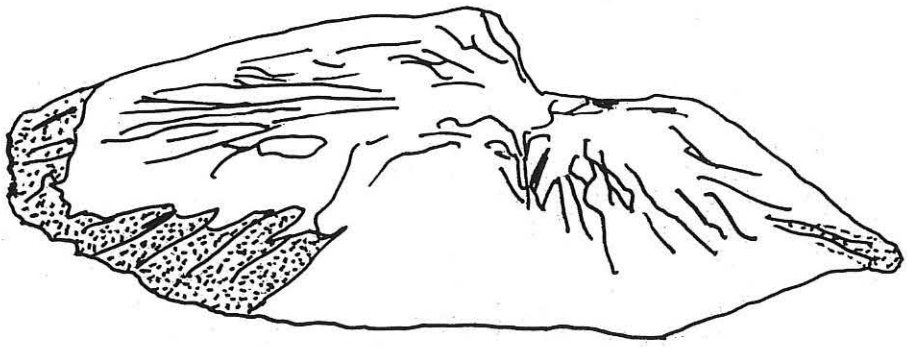


Figure 32. Interoperculum, left lateral (x12).

Figure 32A. *Hymenocephalus italicus*, CS2:6.

Figure 32B. *Coryphaenoides rupestris*, CS2:1.

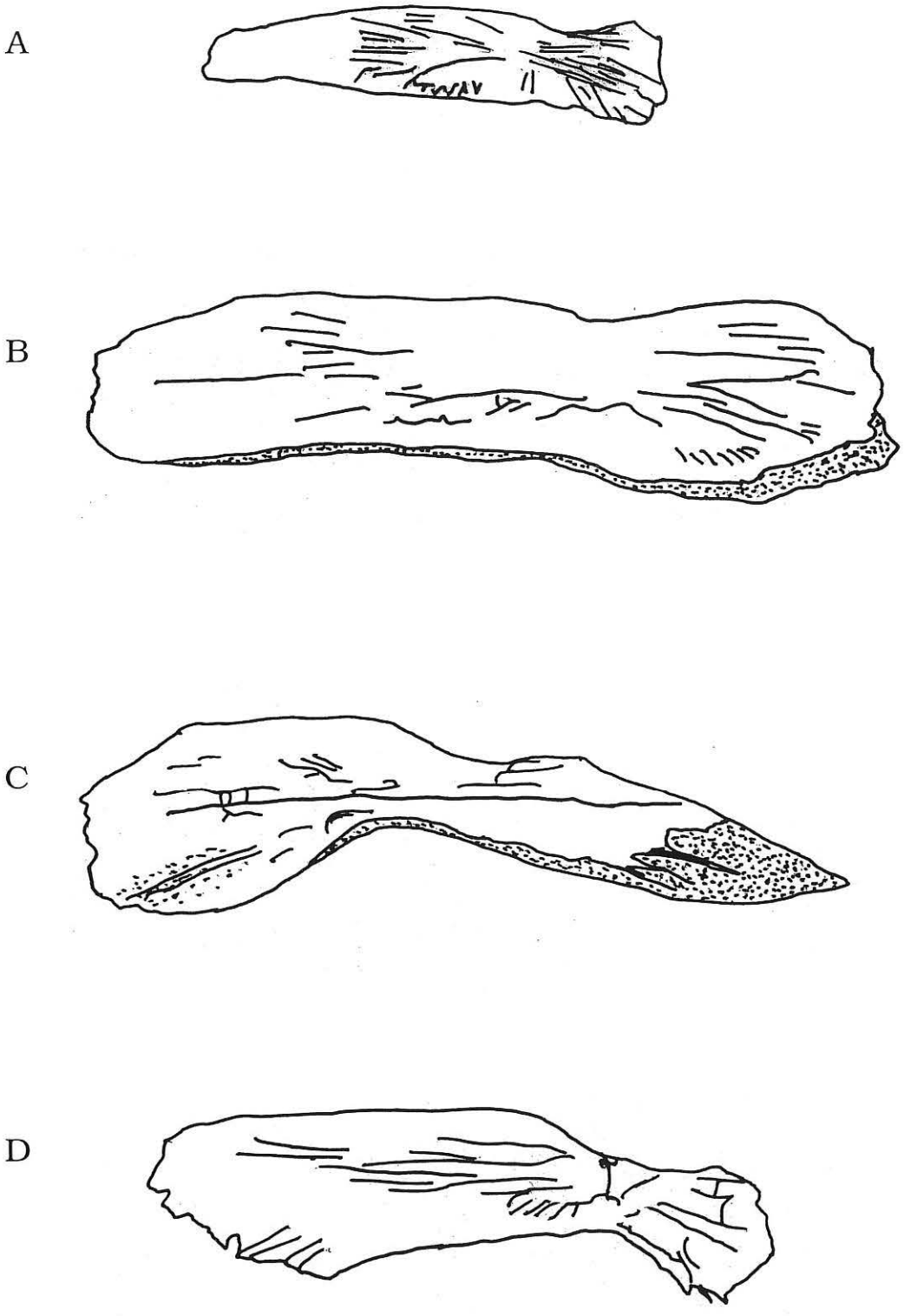


Figure 33. Interoperculum, left lateral.

Figure 33A. (x6) *Chalinura brevibarbis*, CS8:1.

Figure 33B. (x6) *Coryphaenoides zaniophorus*, CS9:1.

Figure 33C. (x12) *Nematonurus armatus*, CS4:3.

Figure 33D. (x12) *Lionurus filicauda*, CS2:3.

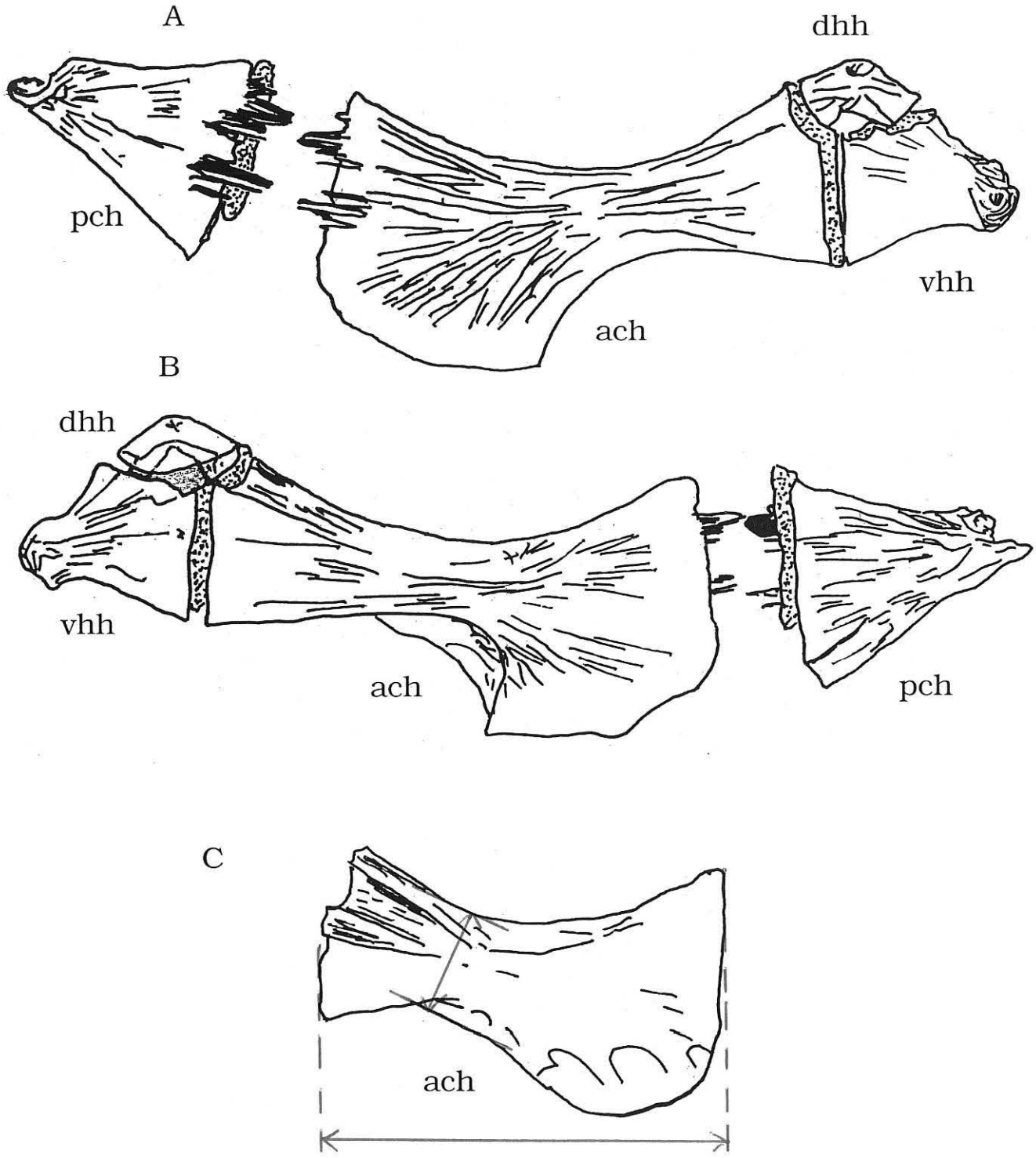


Figure 34. Left hyoid arch (x12).

Figure 34A, B. Medial, lateral, *Malacocephalus laevis*, CS7:3.

Figure 34C. Lateral, *Coryphaenoides mexicanus*, CS9:8.

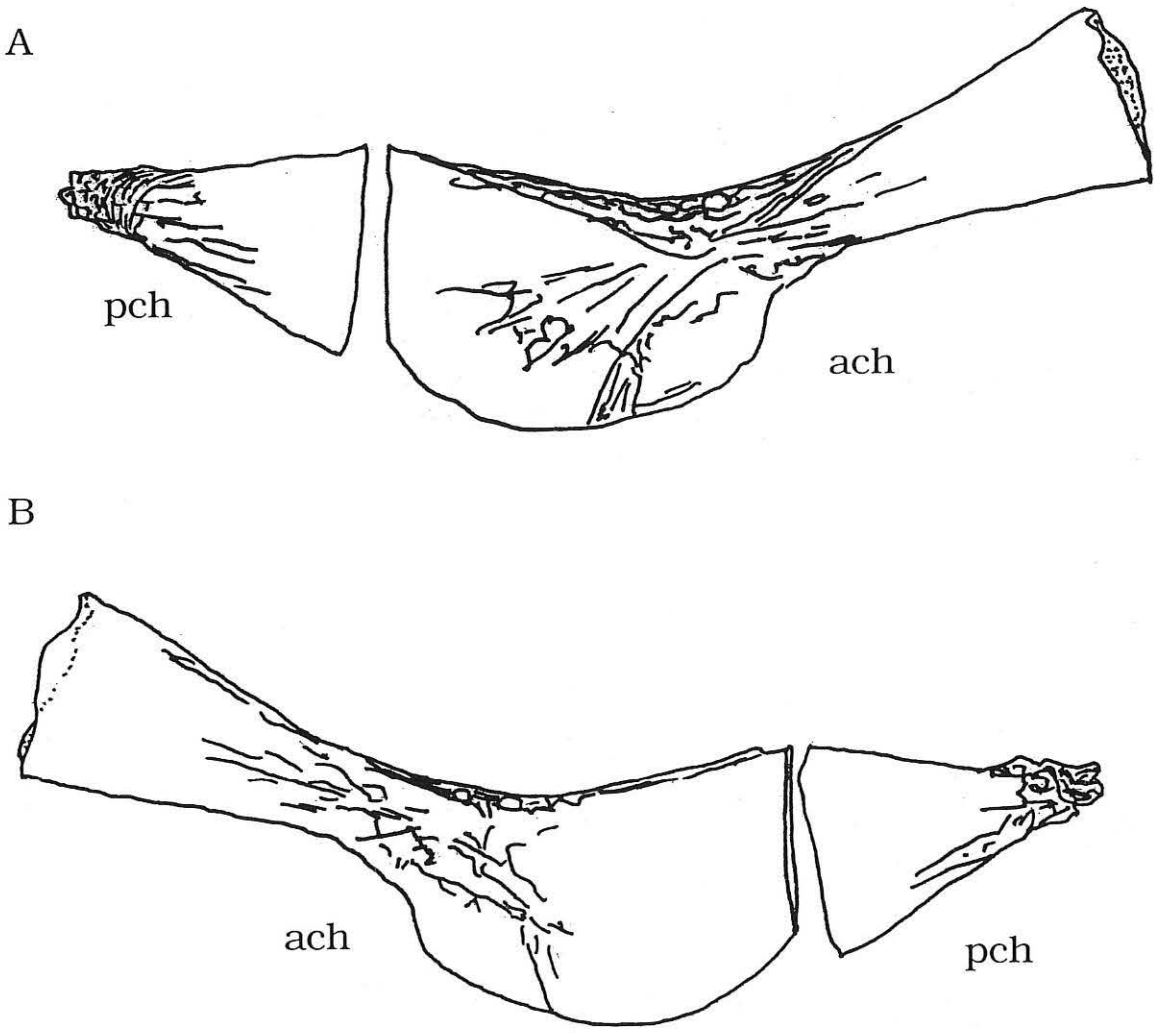
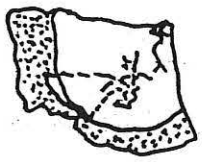


Figure 35. Ceratohyals (x12) *Hymenocephalus italicus*, CS2:6.

Figure 35A. Left medial.

Figure 35B. Left lateral.

A



B

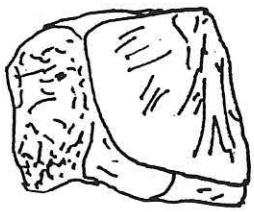
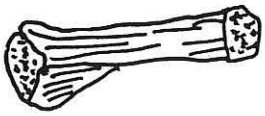


Figure 36. Dorsal hypohyal, left medial (x12)

Figure 36A. *Coryphaenoides rupestris*, CS1:1.

Figure 36B. *Macrourus berglax*, CS7:4.

A



B

Figure 37. Interhyal, left medial.

Figure 37A. (x6) *Macrourus berglax*, CS7:4.

Figure 37B. (x12) *Nematonurus armatus*, CS4:3.

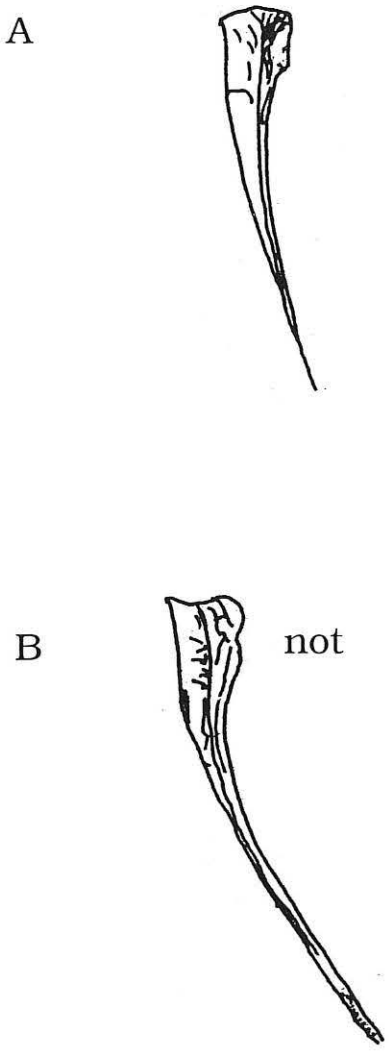
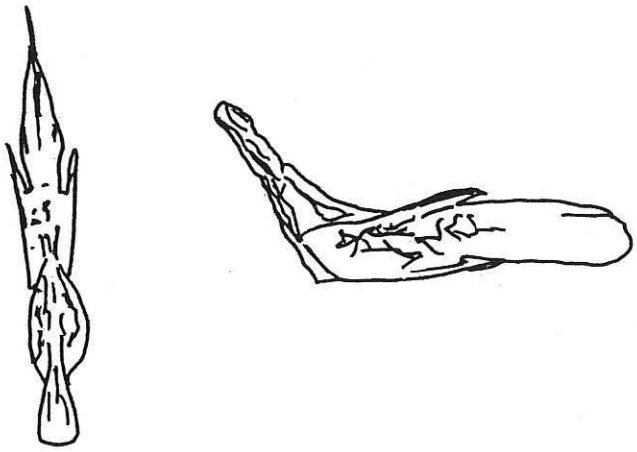


Figure 38. Fourth branchiostegal ray, left lateral (x6).

Figure 38A. *Hymenocephalus italicus*, CS2:6.

Figure 38B. *Coryphaenoides rupestris*, CS1:1.

A



B

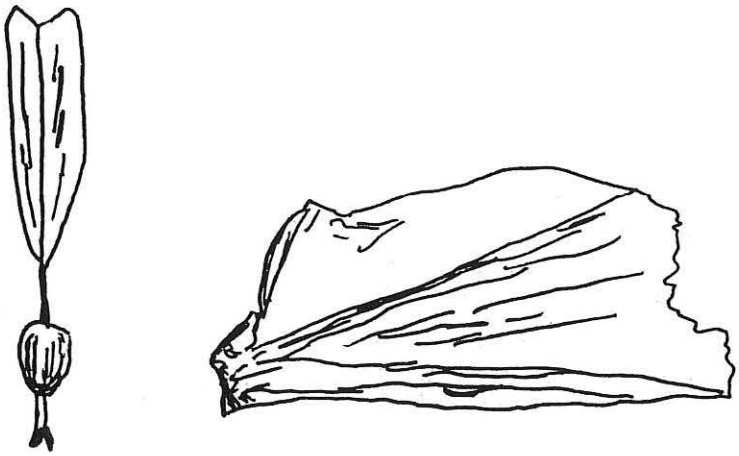


Figure 39. Urohyal, dorsal and left lateral (x12).

Figure 39A. *Melanonus zugmayeri*, GJH.

Figure 39B. *Coryphaenoides rupestris*, CS1:1.

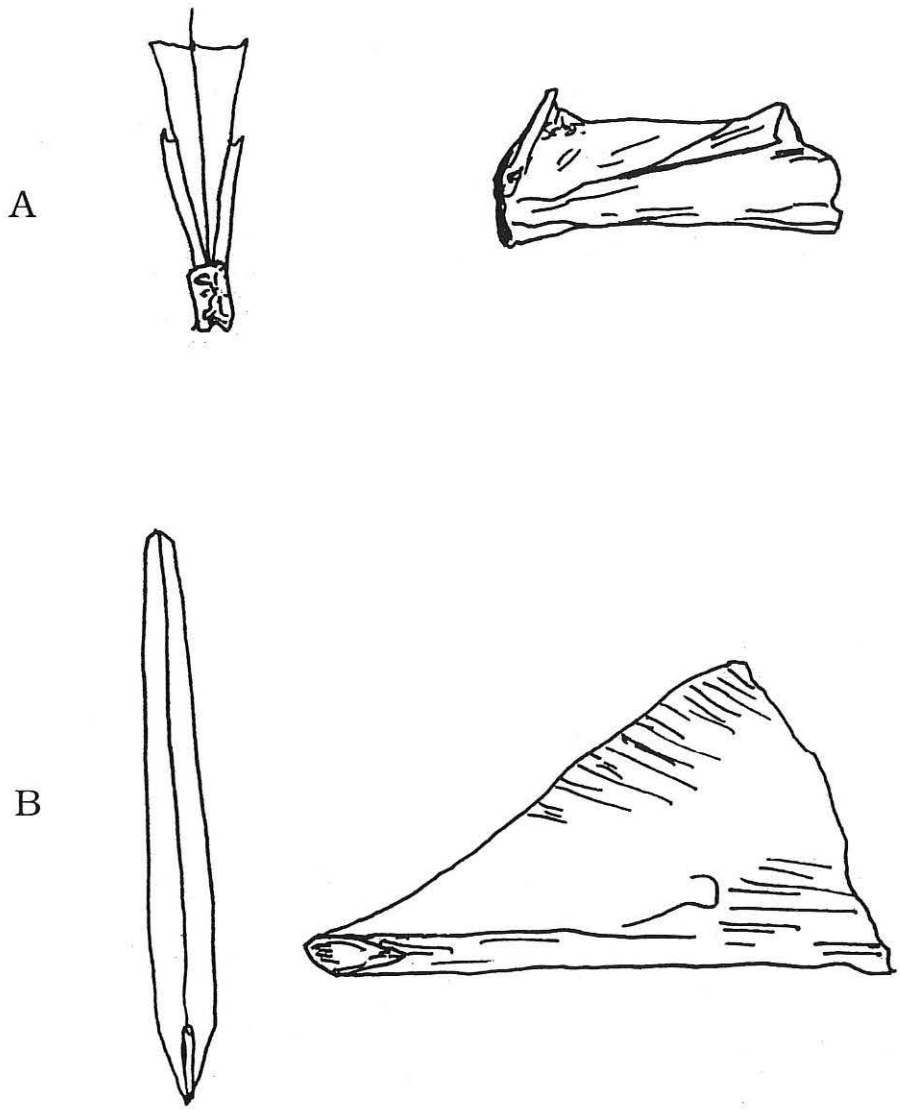


Figure 40. Urohyal, dorsal and left lateral.

Figure 40A. (x12) *Coryphaenoides guentheri*, CS2:2.

Figure 40B. (x6) *Macrourus berglax*, CS7:4.

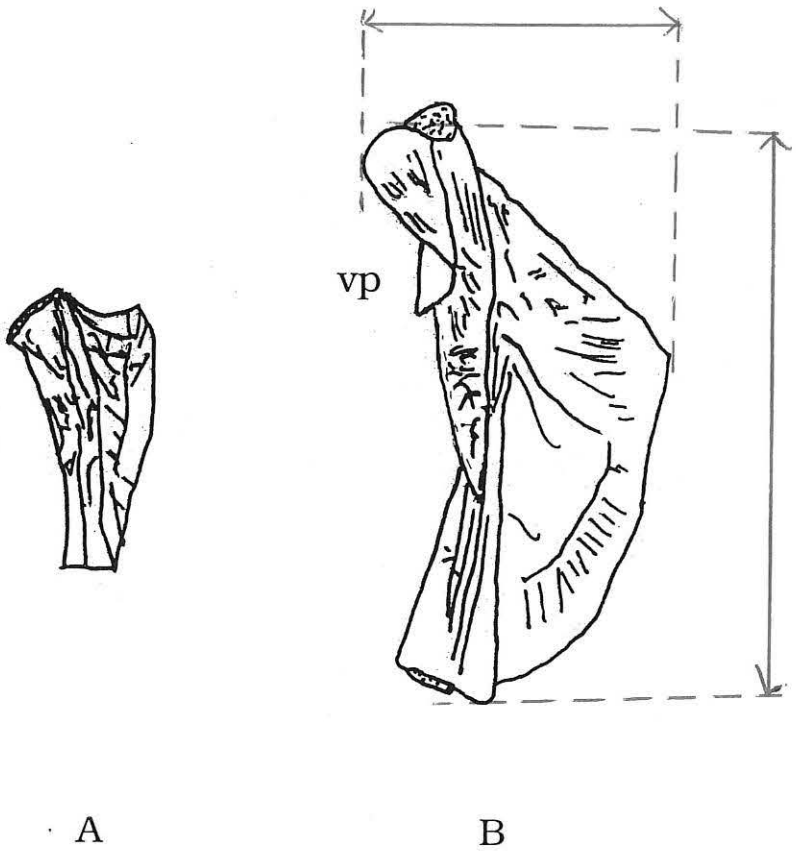


Figure 41. First hypobranchial, left ventral (x12).

Figure 41A. *Coryphaenoides rupestris*, CS2:1.

Figure 41B. *Malacocephalus laevis*, CS4:6.

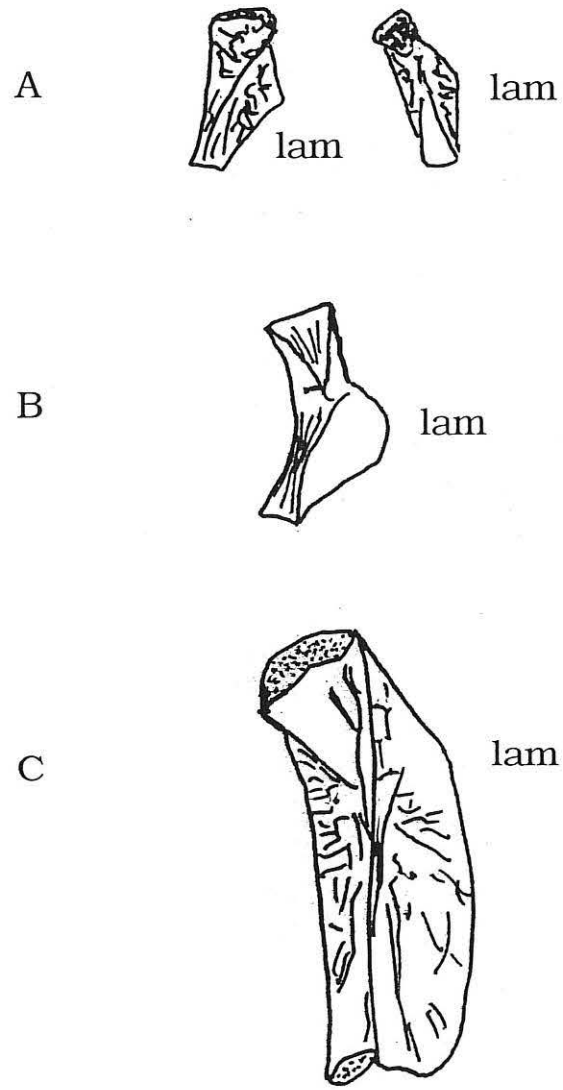


Figure 42. Second hypobranchial, left ventral (x12).

Figure 42A. *Coryphaenoides guentheri*, CS2:2.

Figure 42B. *Sphagemacrurus hirundo*, CS4:4.

Figure 42C. *Malacocephalus laevis*, CS4:6.

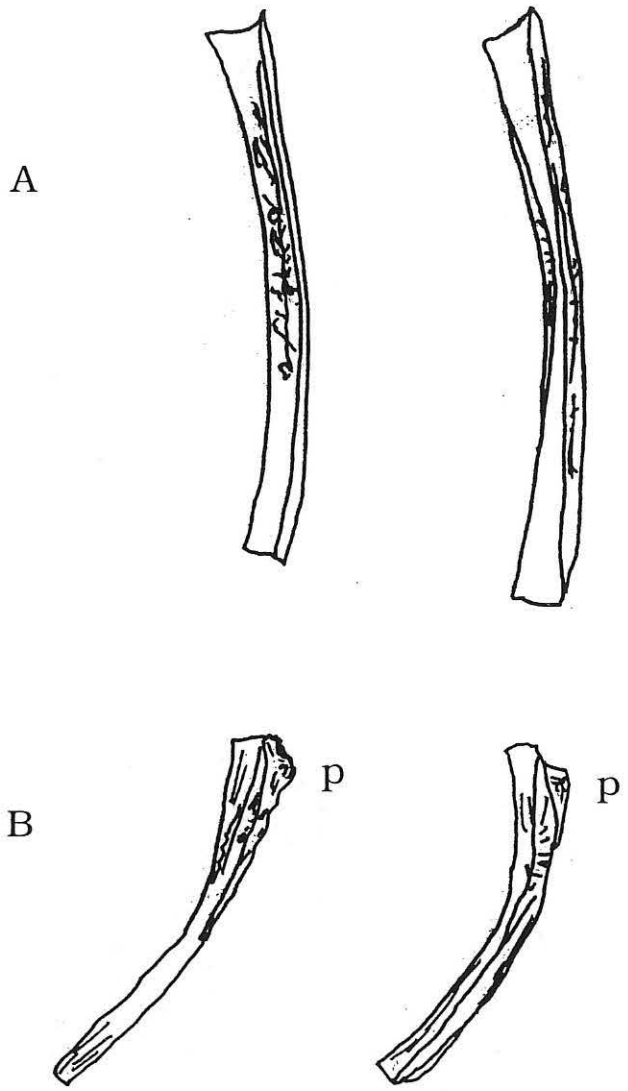


Figure 43. Second and third ceratobranchials, left ventral.

Figure 43A. (x12) *Coryphaenoides rupestris*, CS2:1.

Figure 43B. (x6) *Caelorinchus c. caelorhincus*, CS4:7.

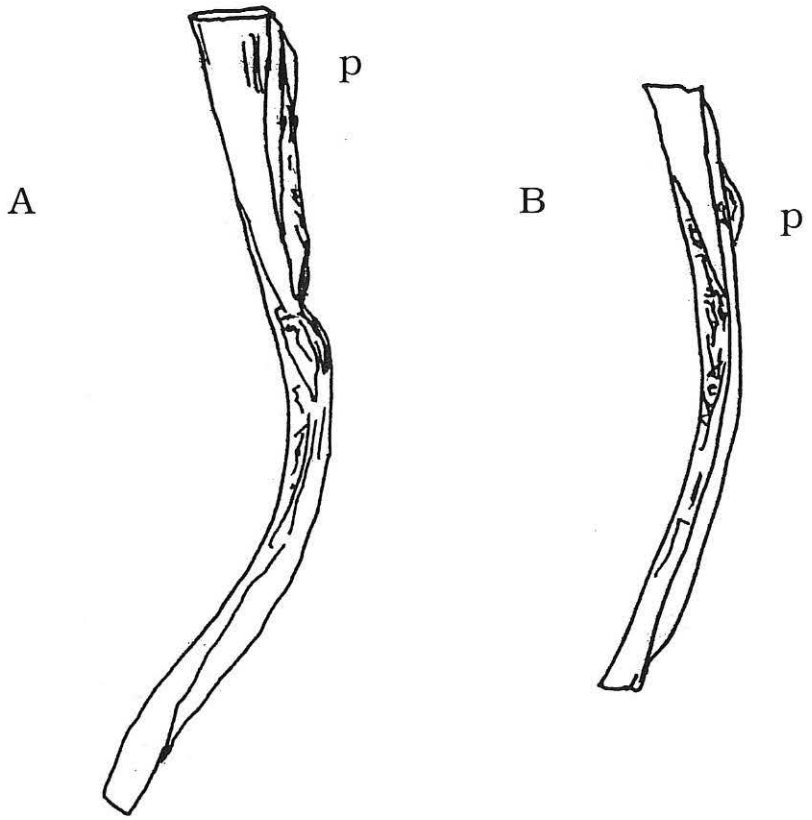


Figure 44. Fourth ceratobranchial, left ventral (x12).

Figure 44A. *Hymenocephalus italicus*, CS2:6.

Figure 44B. *Coryphaenoides rupestris*, CS2:1.

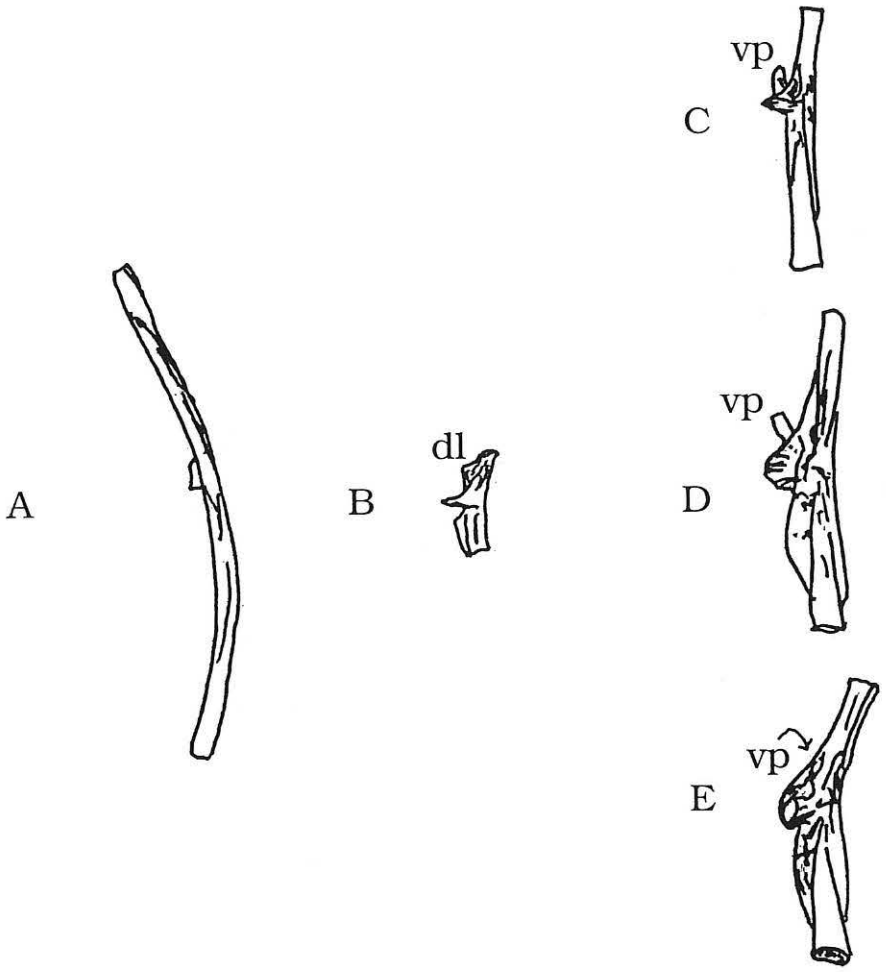


Figure 45. First epibranchial, left ventral.

Figure 45A. (x12) *Hymenocephalus italicus*, CS2:6.

Figure 45B. (x6) *Caelorinchus c. caelorhincus*, CS4:7.

Figure 45C. (x12) *Coryphaenoides rupestris*, CS2:1.

Figure 45D. (x12) *Lionurus filicauda*, CS2:3.

Figure 45E. (x6) *Malacocephalus laevis*, CS4:6.

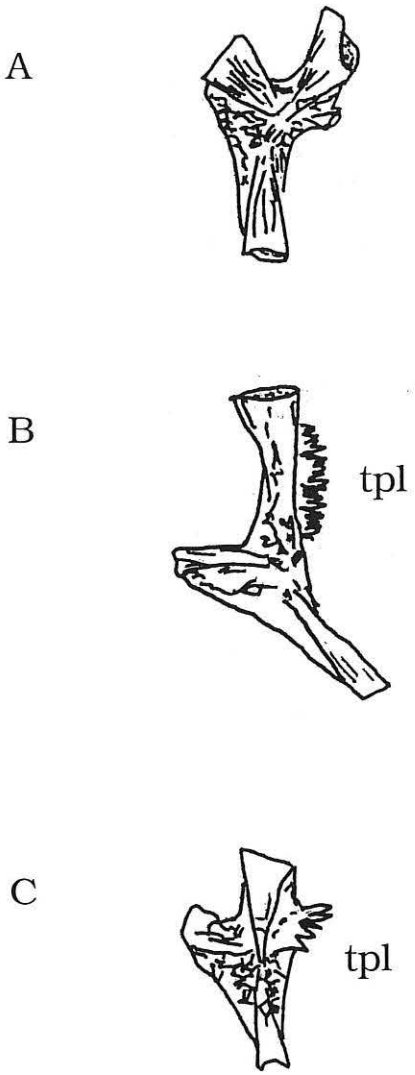
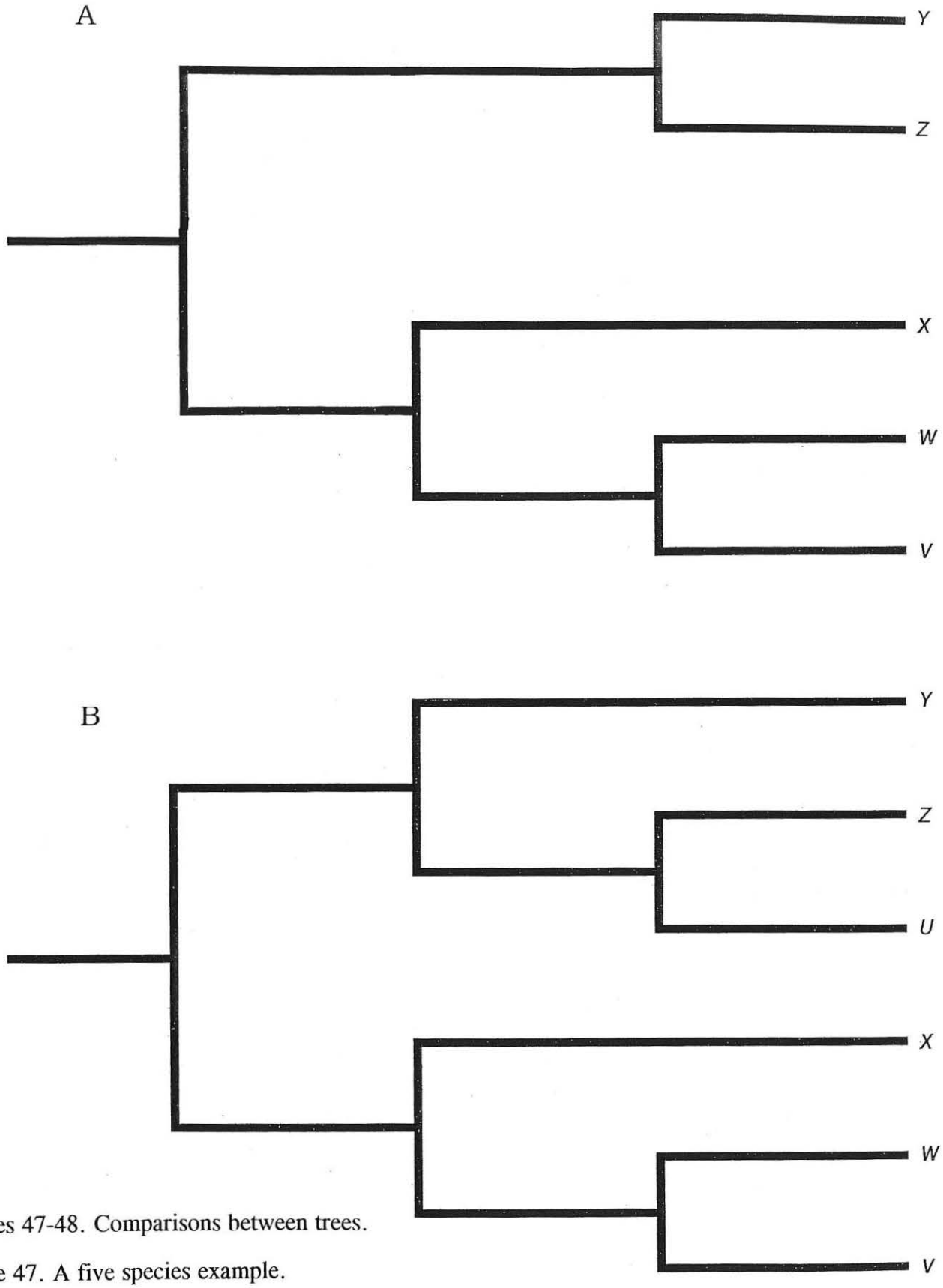


Figure 46. Third epibranchial, left ventral.

Figure 46A. (x6) *Malacocephalus laevis*, CS4:6.

Figure 46B. (x12) *Hymenocephalus italicus*, CS2:6.

Figure 46C. (x12) *Coryphaenoides rupestris*, CS2:1.



Figures 47-48. Comparisons between trees.

Figure 47. A five species example.

Figure 47A. In the most parsimonious tree, the group G consists of species V and W and contrasts with species X, Y and Z.

Figure 47B. In the most parsimonious tree, group G' is not corroborated. Species U nests as the sister group to species Z.

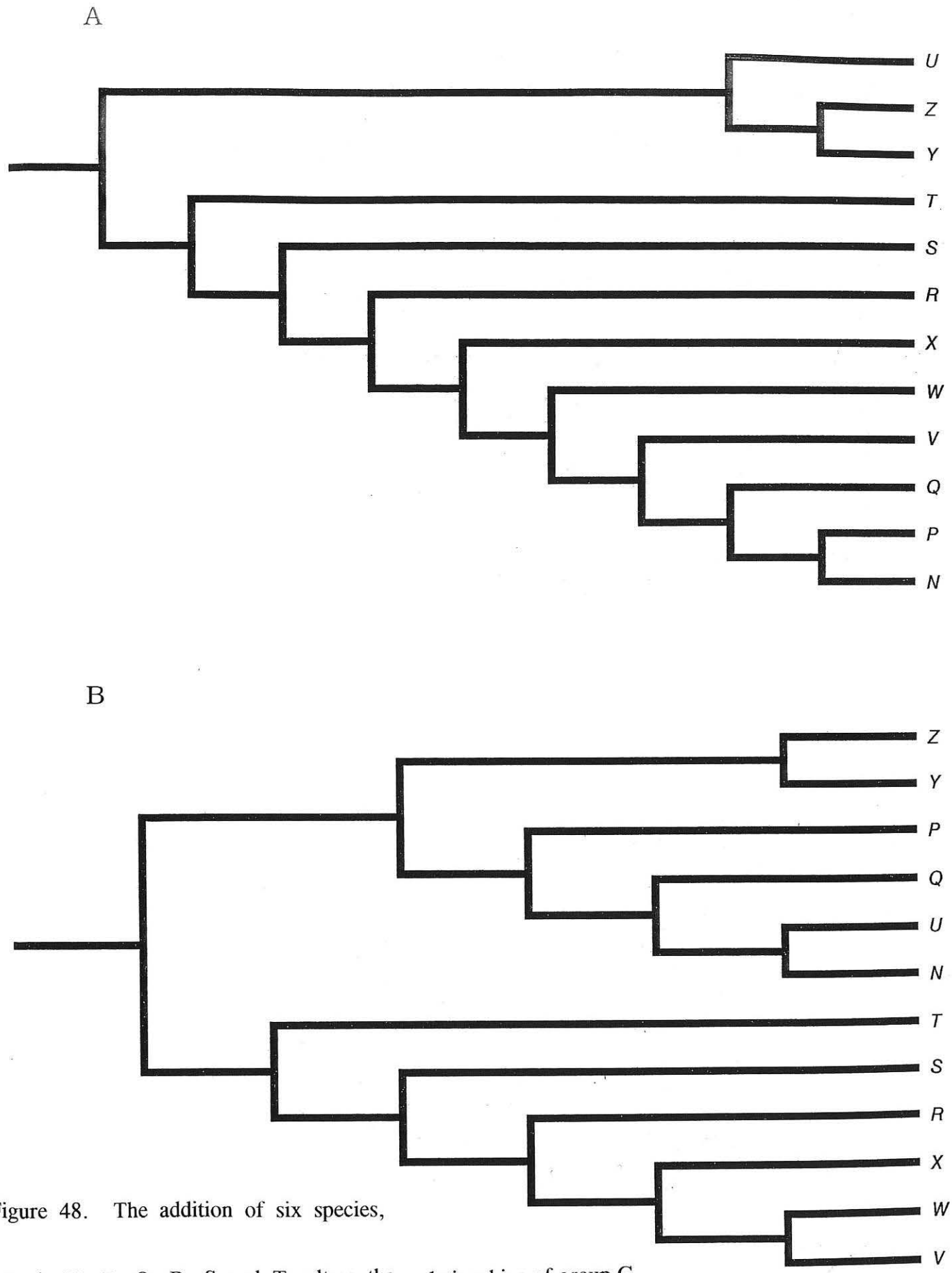


Figure 48. The addition of six species, namely N, P, Q, R, S and T, alters the relationships of group G.

Figure 48A. Group G now includes species N, P and Q as well as species V and W. U has become the sister group of Z and Y.

Figure 48B. Species N, P and Q are no longer a monophyletic group within G. They nest as a group paraphyletic with respect to U.

C

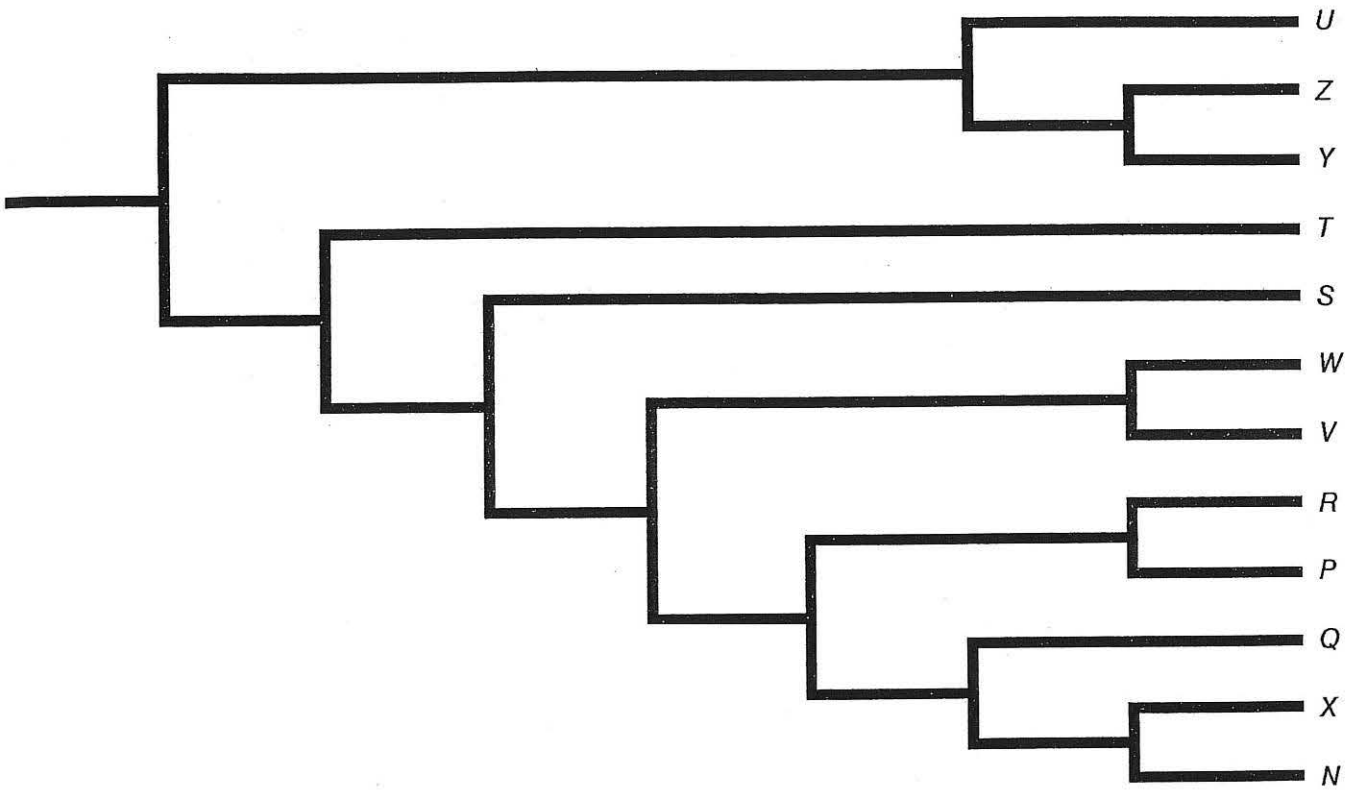
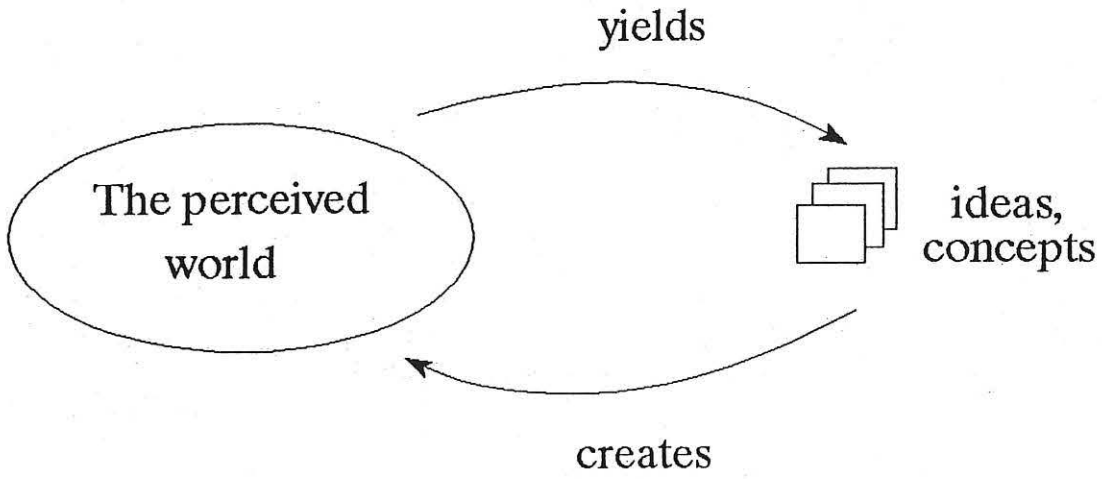


Figure 48C. Species R and X nest within group G.



Figures 49-53. Cladistic analysis as a three-stage process of creation and discovery.

Figure 49. The creation-discovery cycle.

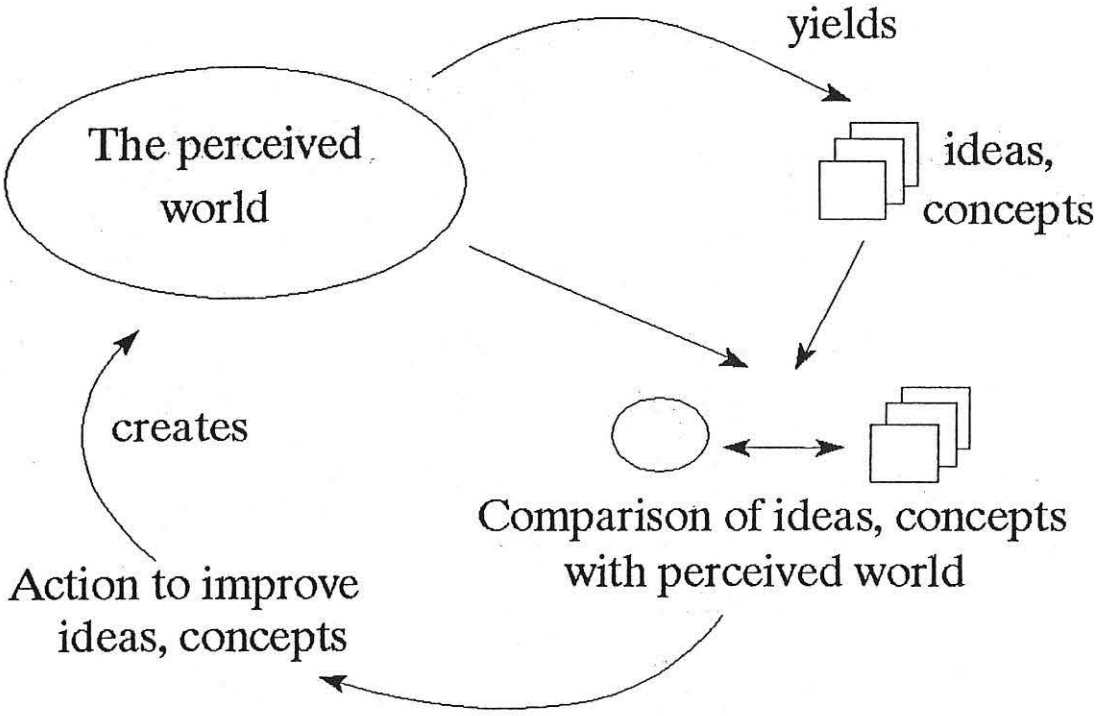


Figure 50. Figure 49 modified to include empirical correction of ideas.

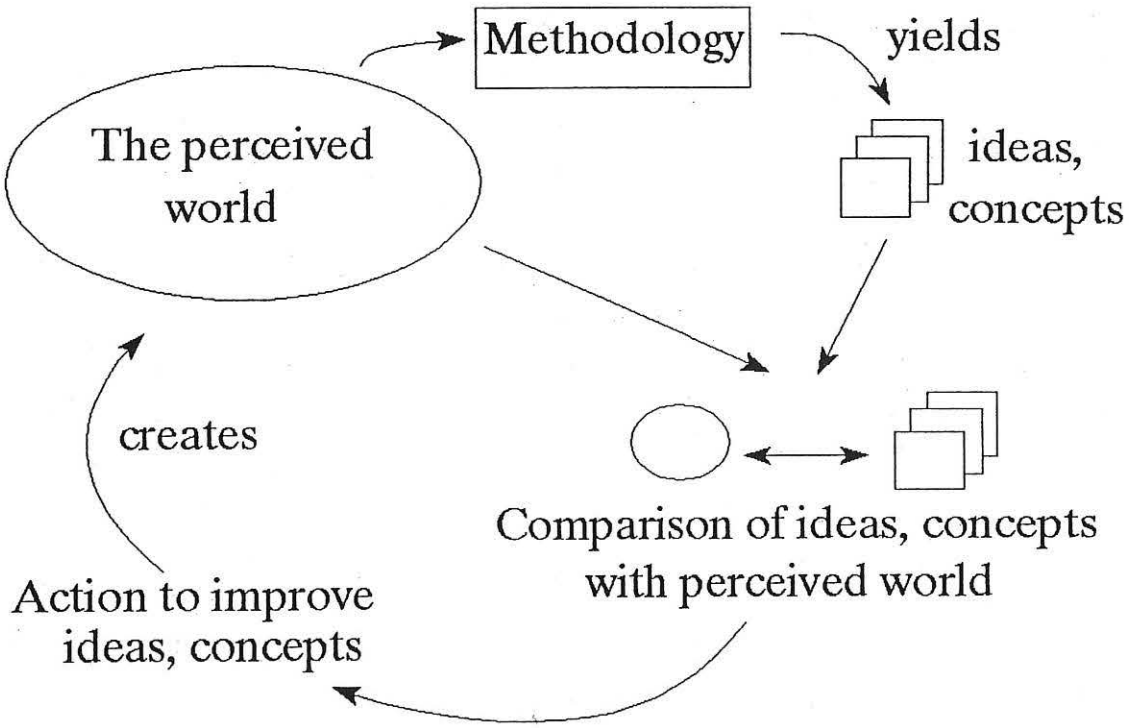


Figure 51. Figure 50 modified to include use of a scientific methodology.

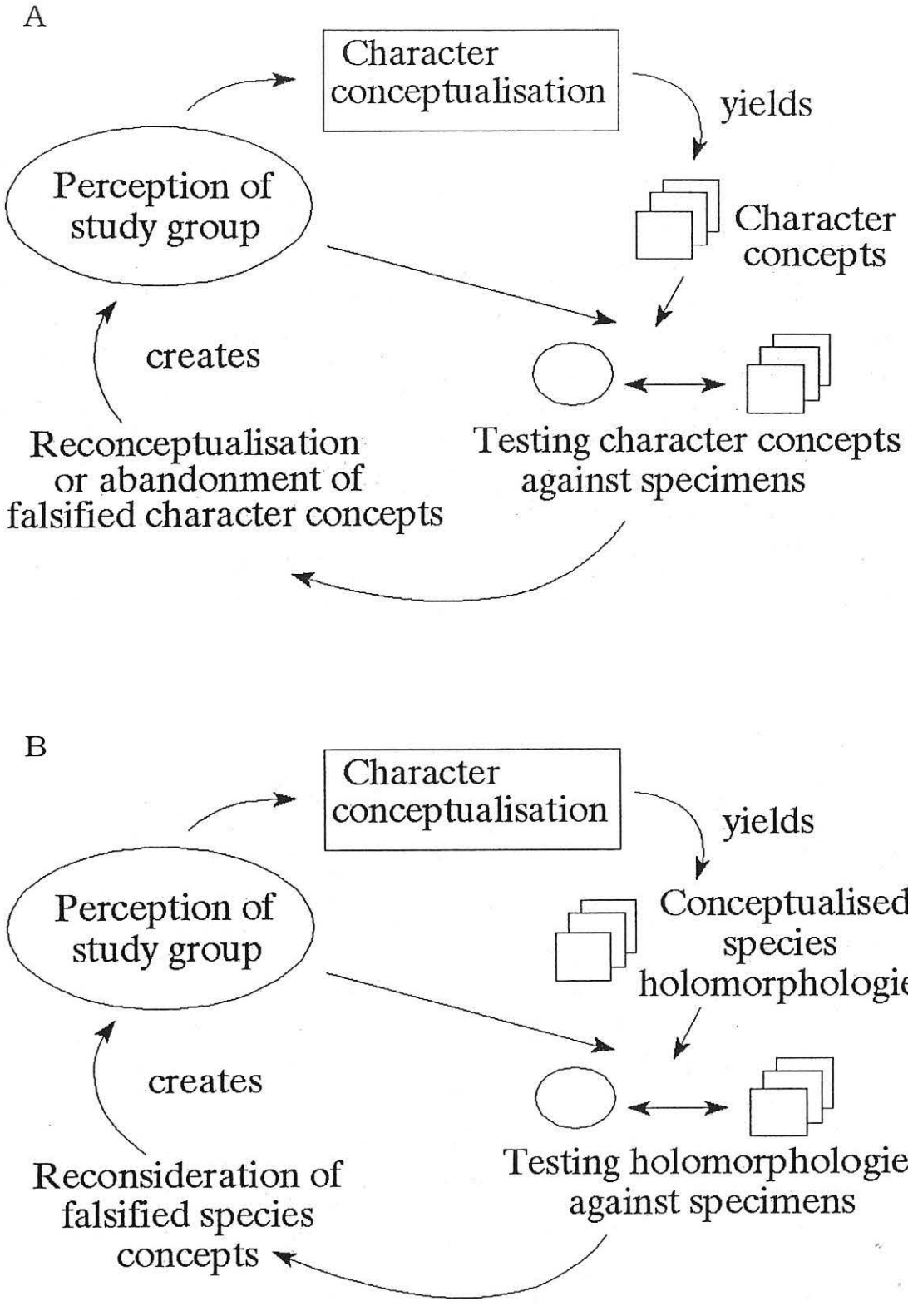
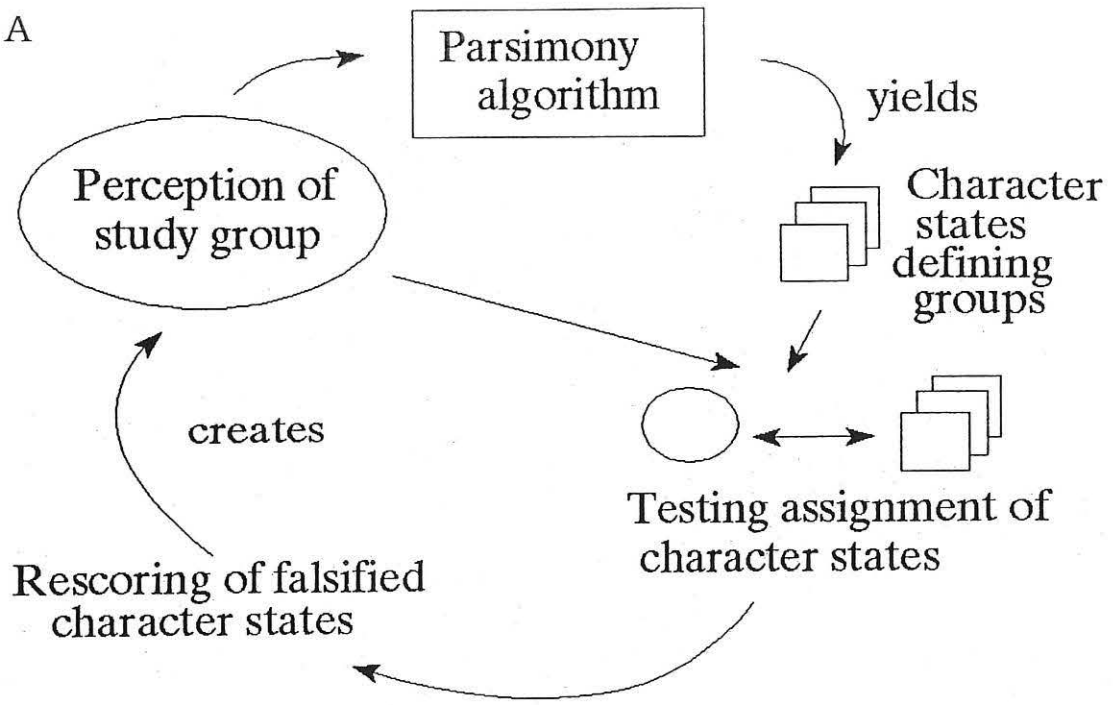


Figure 52. The derivative stage of cladistic analysis: character conceptualisation.

Figure 52A. Proposition and testing of character concepts.

Figure 52B. Character conceptualisation leads to a reconsideration of species concepts.



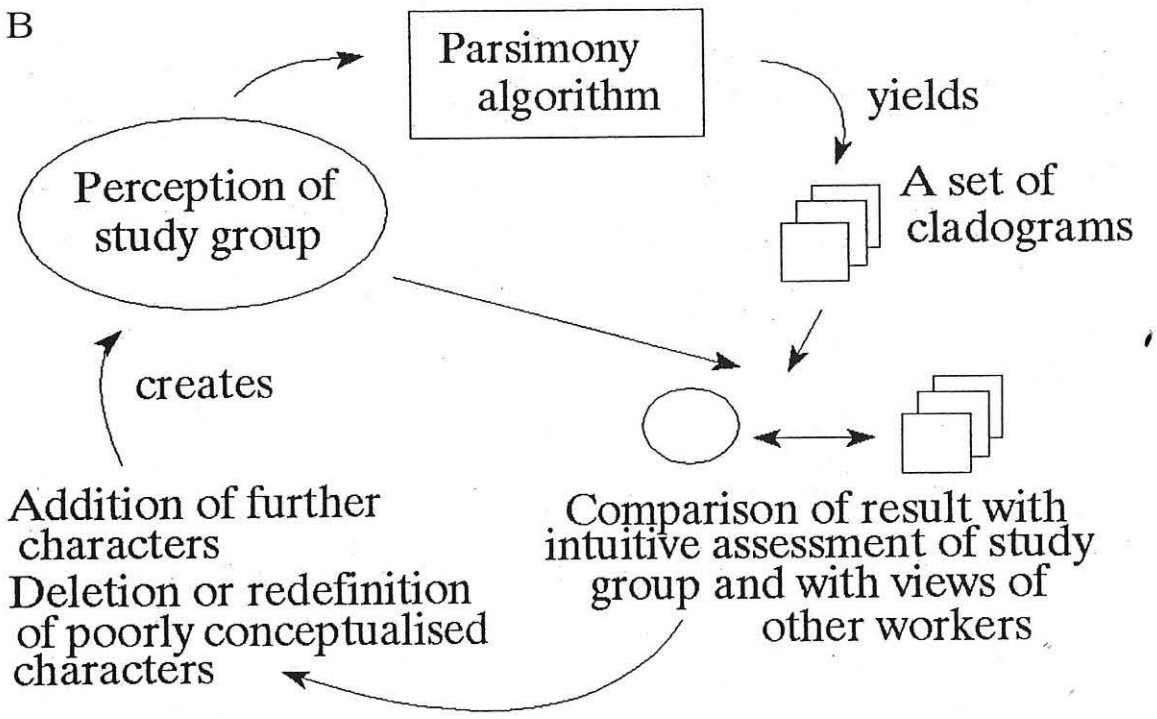


Figure 53. The general stage of cladistic analysis: parsimony analysis.

Figure 53A. Assignment of character states to groups and possible rescoring of falsified character states.

Figure 53B. Assessment of result leading to addition of further characters or to deletion or redefinition of poorly conceptualised characters.

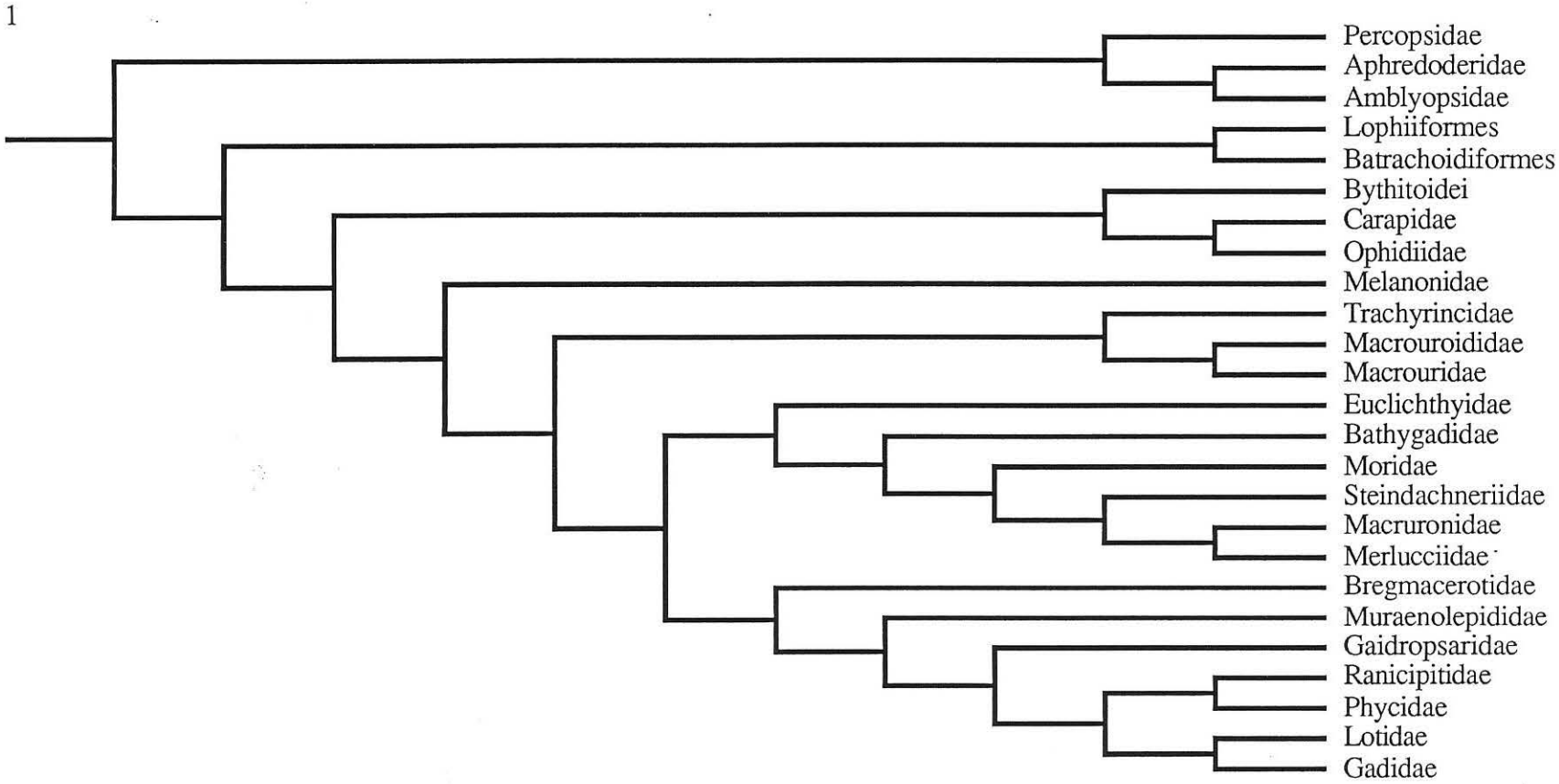


Figure 54. Results of WOGADS analysis.

Figure 54A. Two most parsimonious trees.

2

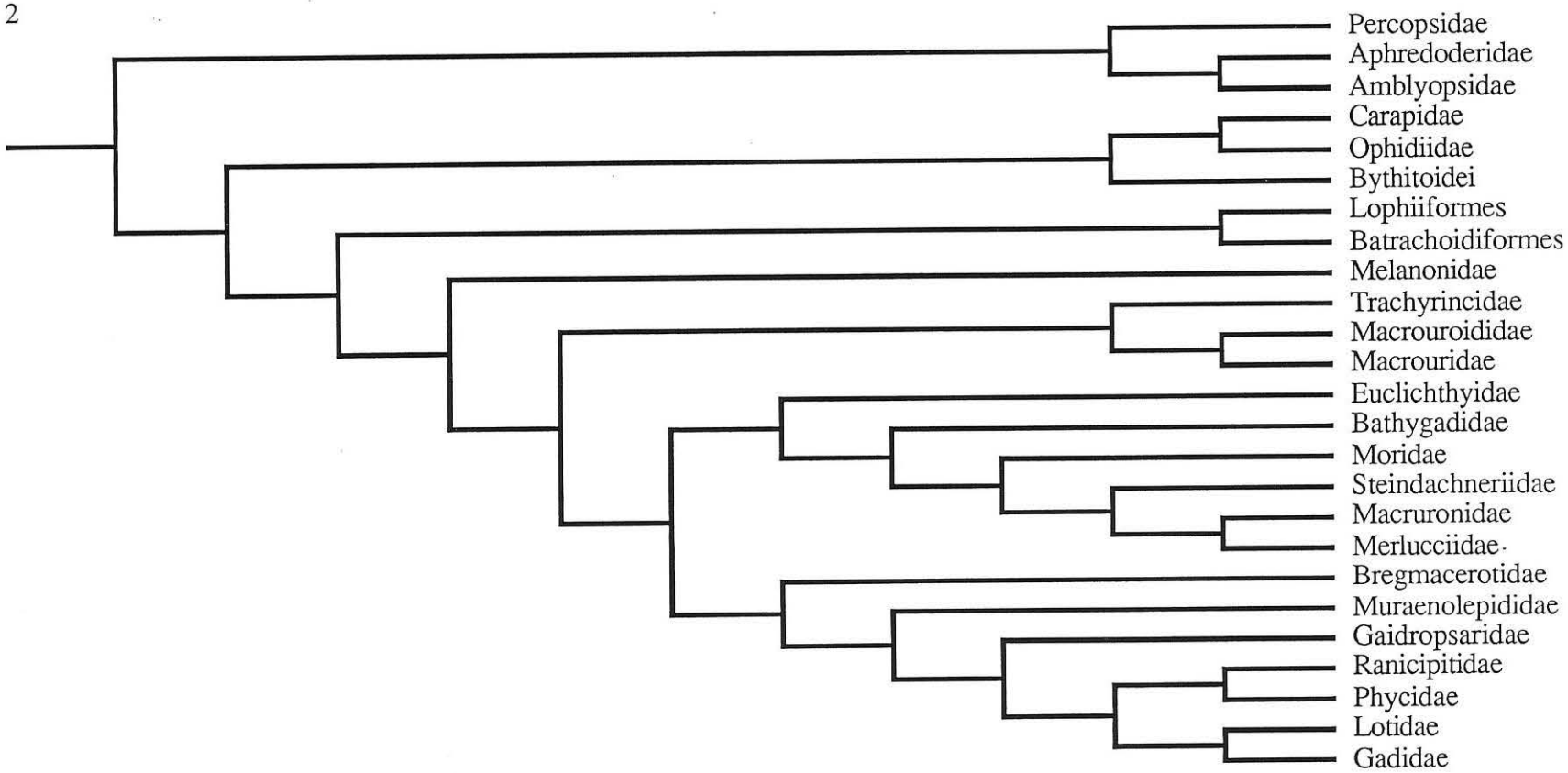


Figure 54A. (continued)

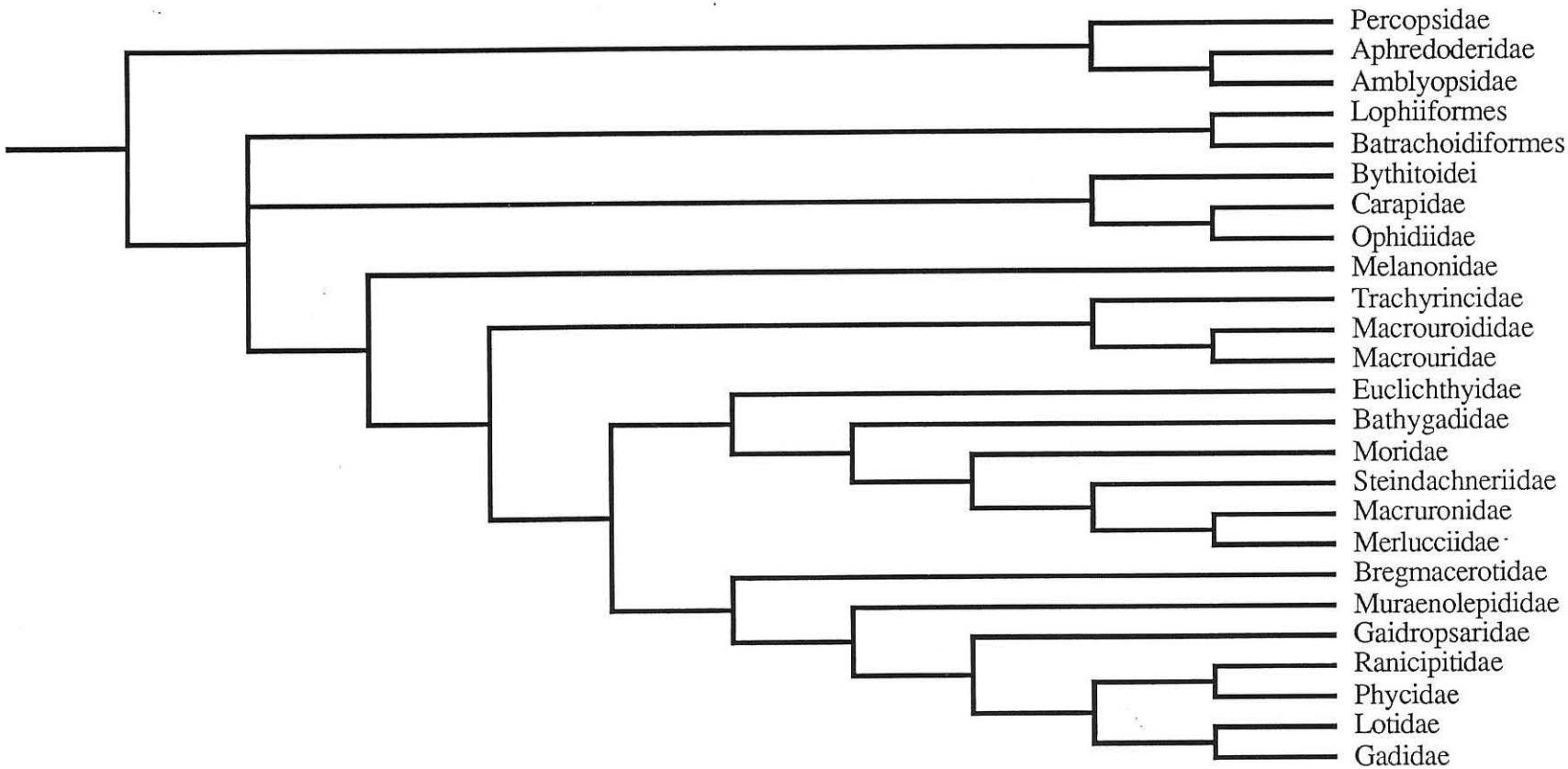
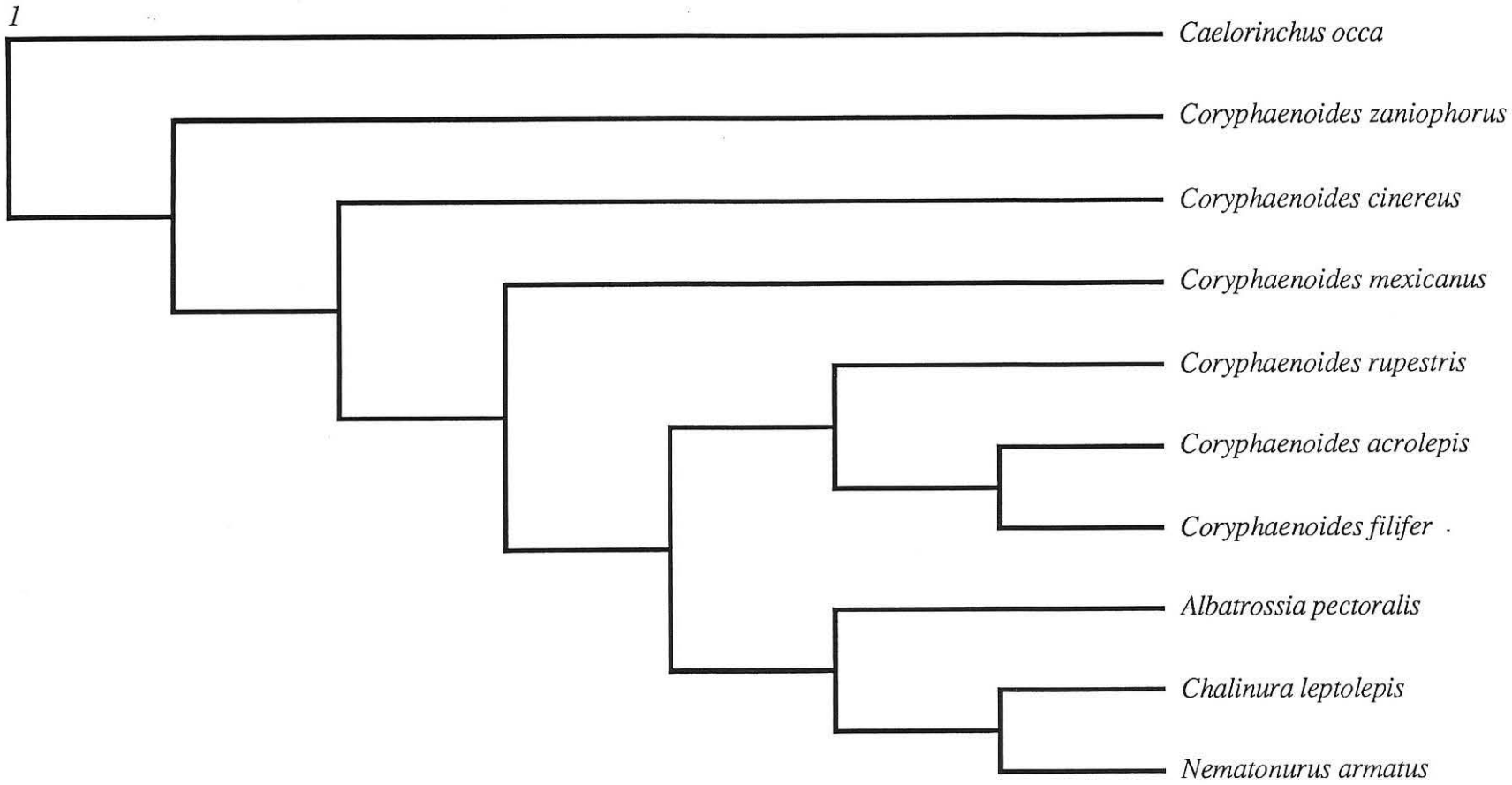


Figure 54B. Strict consensus.



Figures 55-57. Results of rattail analysis.

Figure 55. Peptide mapping data from Wilson, Siebenaller and Davis (1991): two most parsimonious trees.

Figure 55A. Trees rooted at *Caelorinchus occa*..

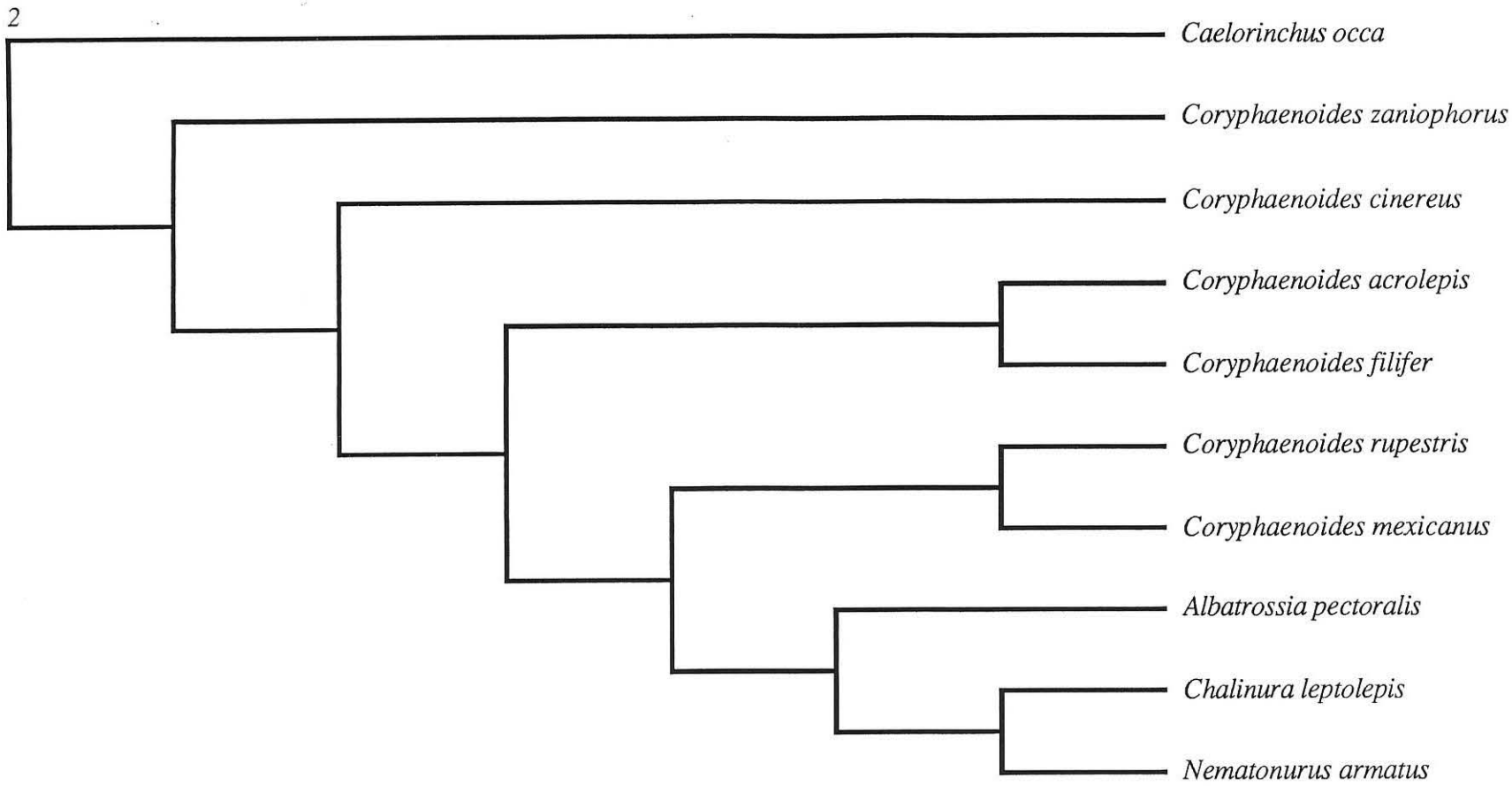


Figure 55A. (continued)

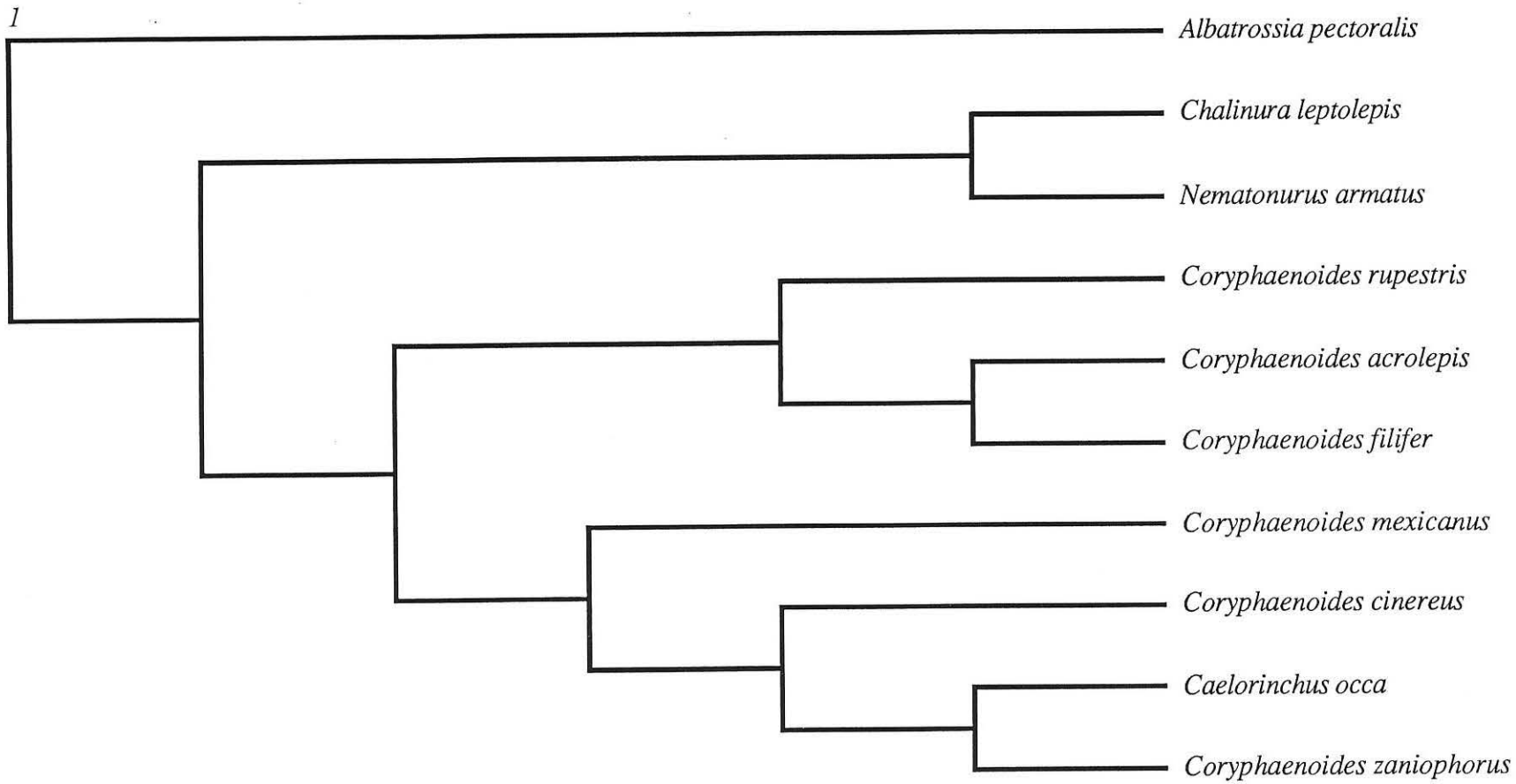


Figure 55B. Trees rooted at *Albatrossia pectoralis*..

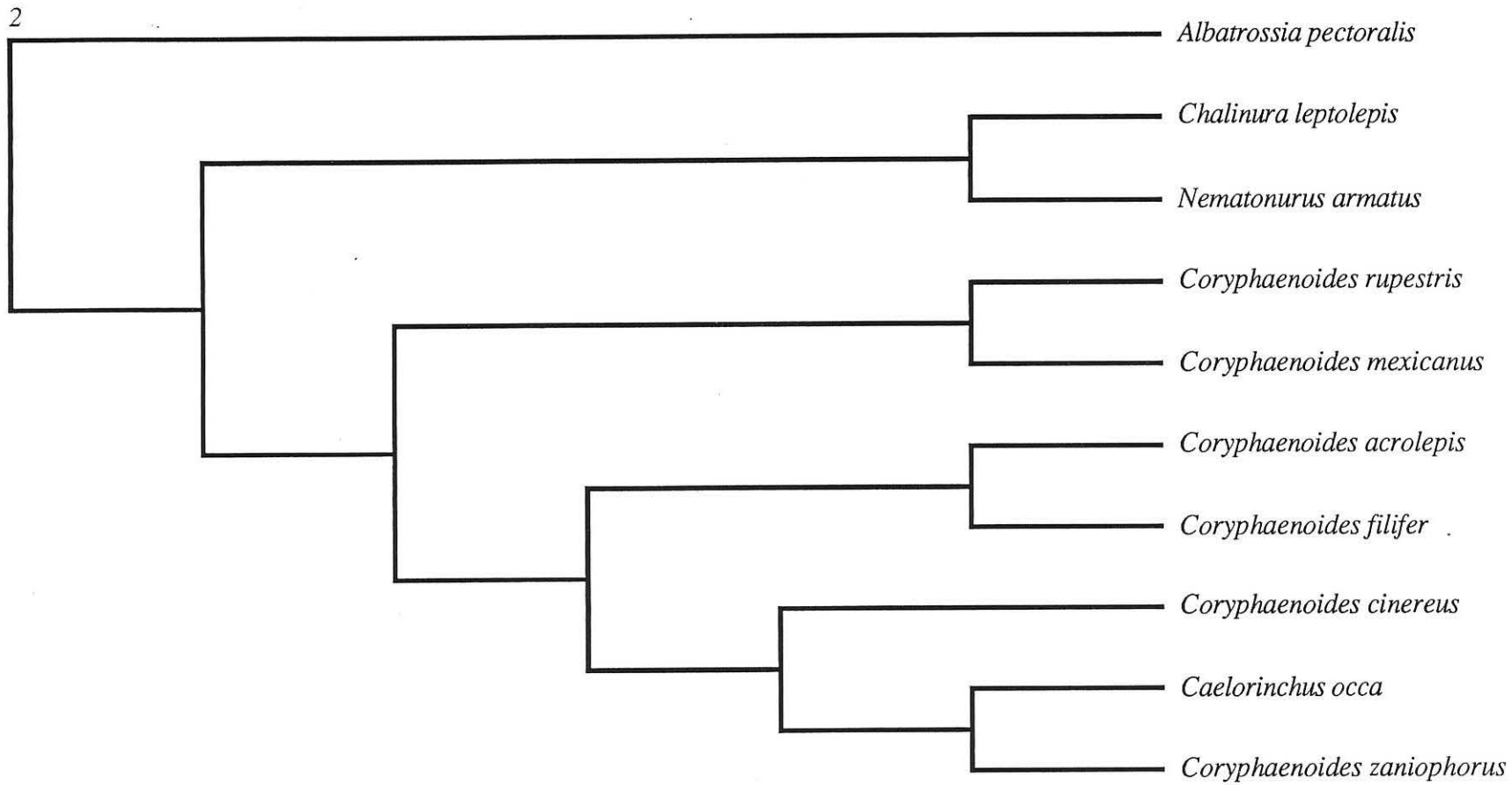


Figure 55B. (continued)

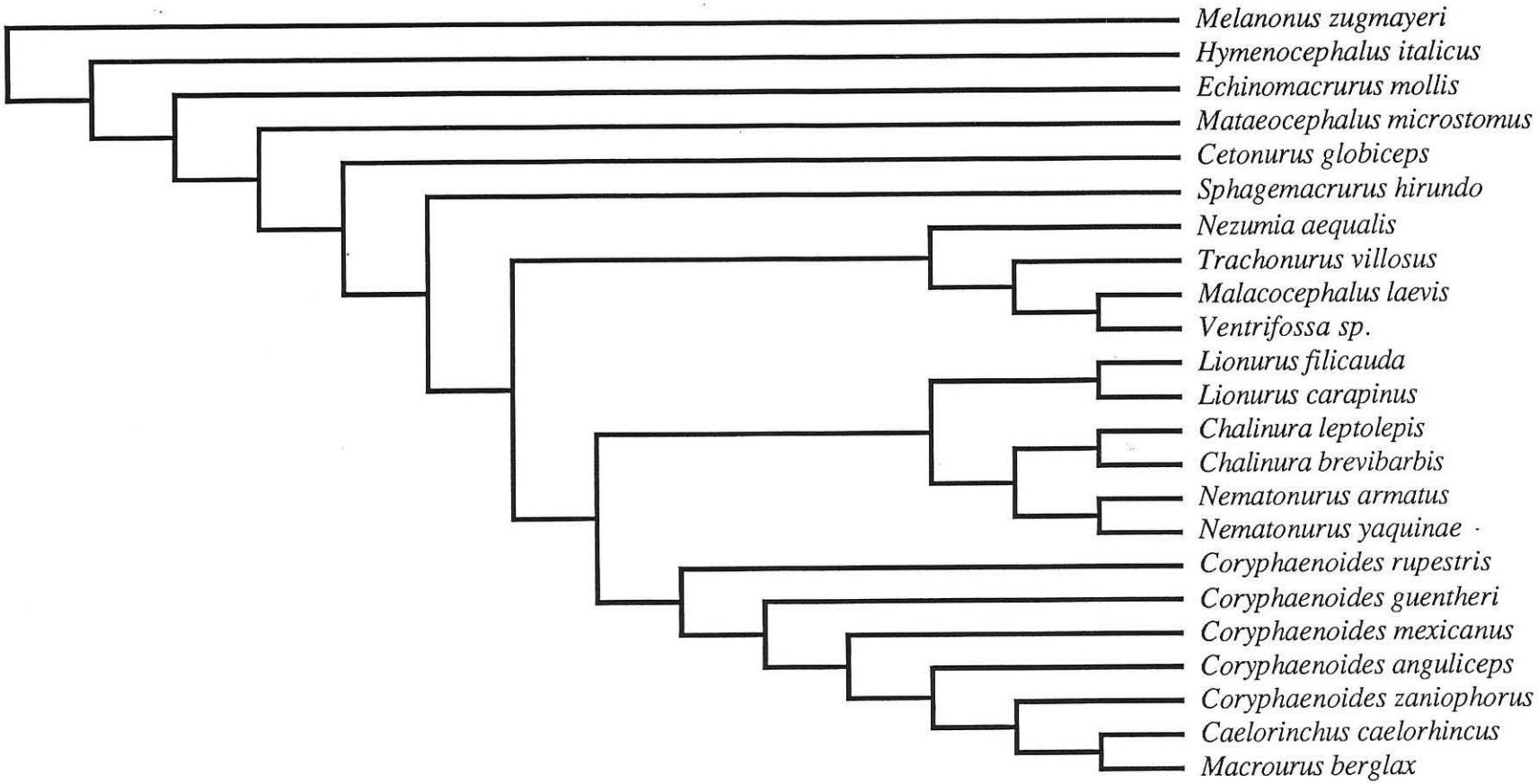


Figure 56. Morphological data: single most parsimonious tree.

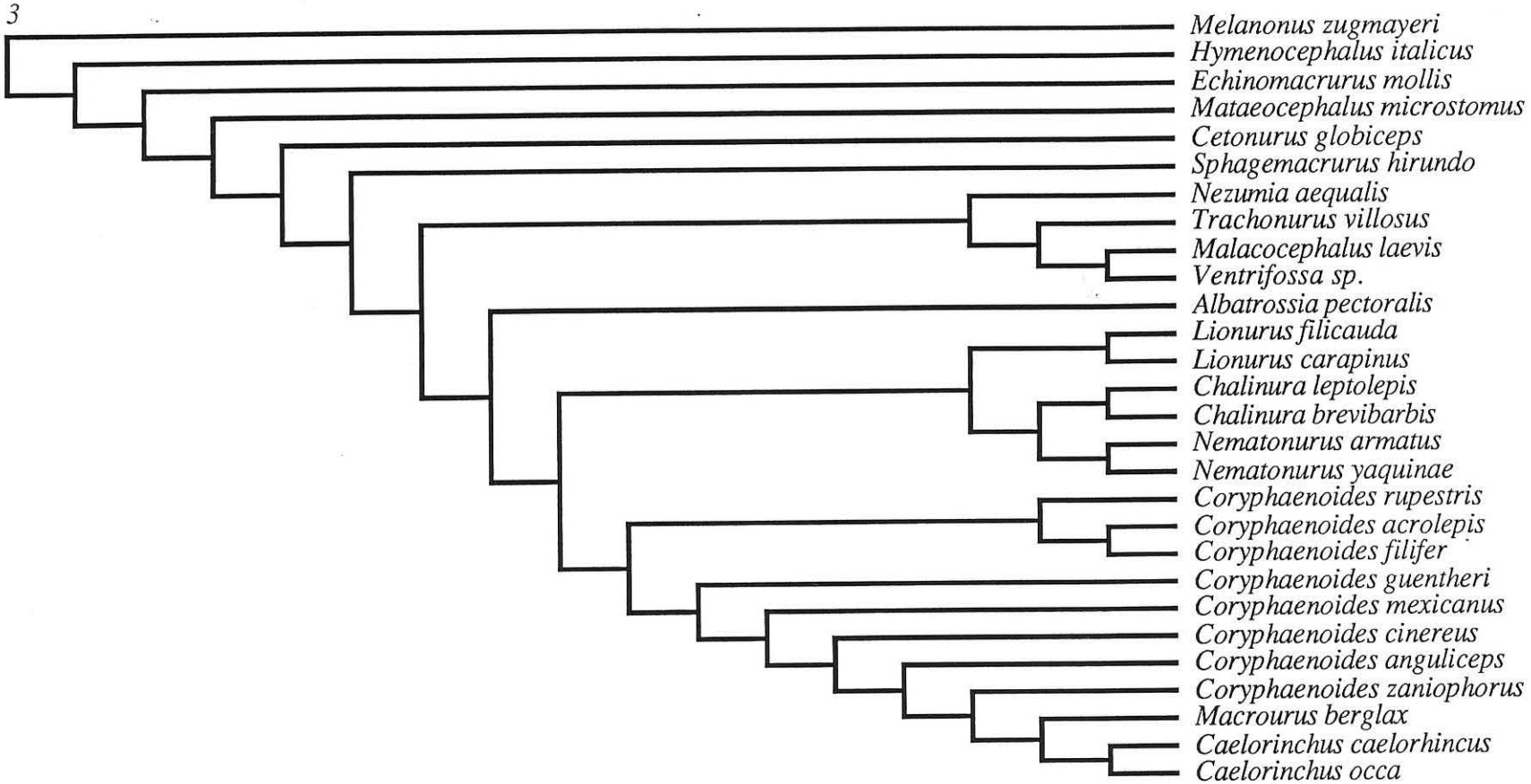


Figure 57A. (continued)

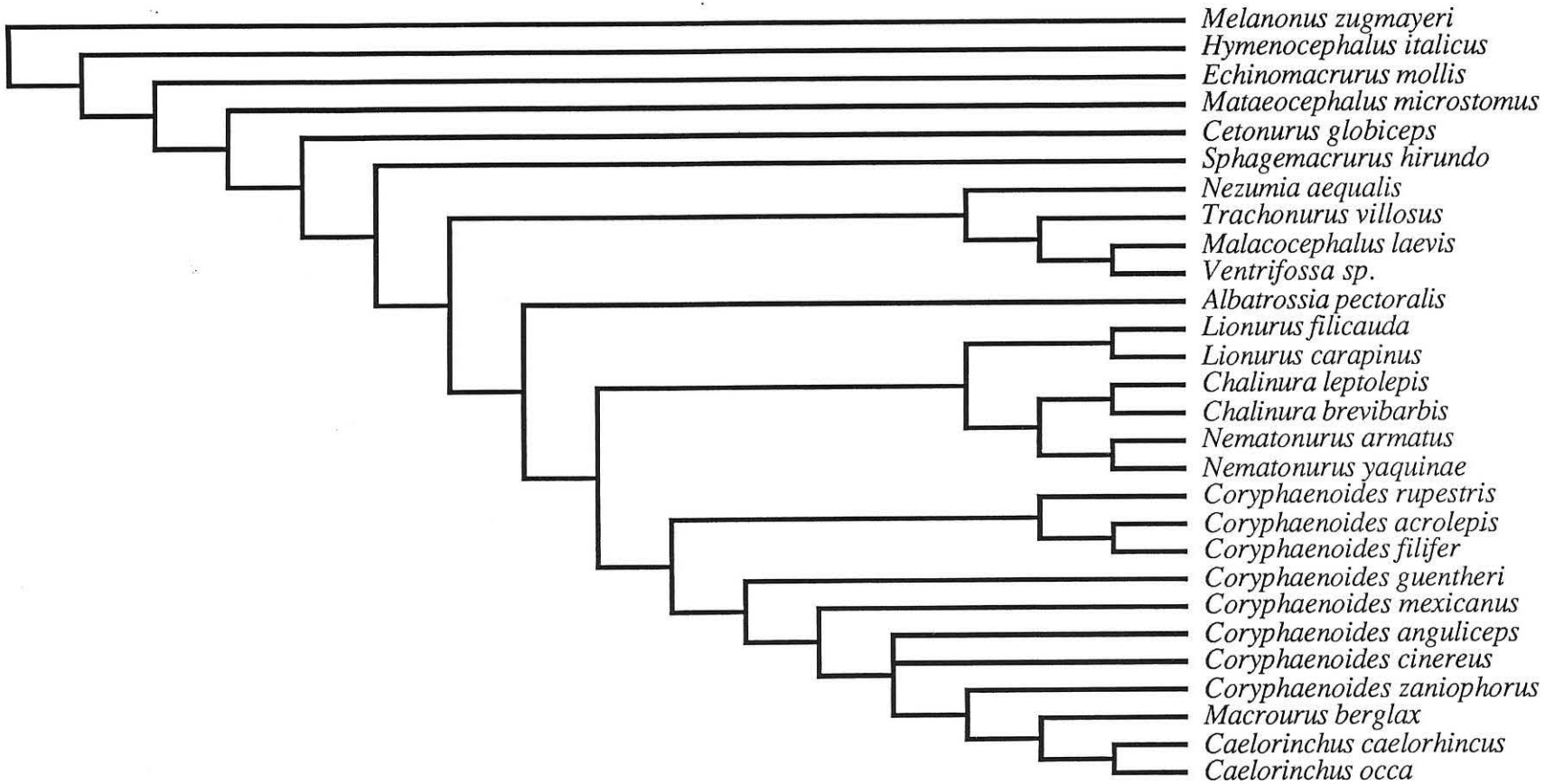


Figure 57B. Strict consensus.